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REVIEW

Female Reproduction in Malacostracan Crustacea

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INTRODUCTION

As in most organisms, the series of complex events that render the female germ cell of crustaceans capable of conjugation with the spermatozoon evolves over a long period which extends from the time of oogonial differentiation to the final maturation of the oocyte.

It is now well-known that the study of female reproduction falls into five main areas: 1) the mechanism of ovarian differentiation, 2) the sequence of morphological steps leading to vitellogenesis, oocyte maturation and activation, 3) the endocrine regulation of the onset, completion and maintenance of these different steps, 4) the influence of external factors such as photoperiod, temperature, ionic concentration of sea water on the female gametogenesis, 5) the events that follow mate selection and allow a specific response of the oocyte surface to the spermatozoon for a successful fertilization. Then, the normal growth of the embryo is ensured during incubation, a period of the life span of the female that is associated with the development of external sex characteristics and the secretion of pleopod tegumental glands in some species.

We must point out that the major phenomena that characterize crustacean oogenesis and its regulation need to be known not only for the goal of basic research but also for the benefit of the aquaculture field. Achieving control of reproduction is often identified as a major problem that prevents the potential of shrimp farming from becoming a profitable industry. Thus, for their economical interest, a number of research programs are now devoted to the Decapoda, one of the three most-studied Malacostraca orders beside the Amphipoda and Isopoda.

A few general features related to the knowledge of malacostracan reproduction are recalled hereafter:

1. With the exception of Oxyrhyncha crabs which become sexually mature after a terminal molt, as the majority of insects, most malacostracan Crustacea continue to molt after puberty.

2. In peracarids and natantian decapods, spawning is obligatorily preceded by a molt and, during the period of genital activity, the number of spawnings varies according to the species.

3. Except for penaeid prawns that are free-spawners, malacostracans incubate their eggs. As a matter of fact, the time interval between each spawning is always longer than the time of egg incubation.

4. In species in which the development comprises larval stages, an ovigerous female carries

around several thousands of small sized-eggs (about 250 μm of diameter in the blue crab), whereas in species with abbreviated (direct) development a hundred or less eggs of larger size (about 3500 μm of diameter in the European crayfish) are incubated. Indeed, the loss of eggs due to predators or unfavorable environmental conditions as particularly encountered by the eggs of penaeids, is considerably reduced in malacostracans which have an abbreviated development and spawn in protected areas.

In this paper, we have tried to recapitulate the known processes undergone by the oocyte in order to acquire the capacity to generate the species. As in most animals, the sequence of major morphological transformations that occur during crustacean oogenesis includes the differentiation and the evolution of oogonia into primary oocytes that undergo previtellogenesis, vitellogenesis and meiotic maturation. Then, activation follows fertilization and spawning, physiological events that permit the completion of gametogenesis.

We have included the main features of the sex characteristics associated to the evolution of the female gamete as well as the regulation of these morphological events by hormonal and environmental factors. At last, the adjacent aspects related to sex recognition and mating behavior are briefly surveyed.

It must be noticed that the most intensely investigated aspect of oogenesis concerns the vitellogenesis. The term "vitellogenesis" will be employed in this review in the way it is the most frequently found in the literature referring to the reproductive physiology of egg laying animals, i.e., as synonymous with "secondary vitellogenesis" [1]. We shall see (Section II, A, 1) that this conspicuous event corresponds to a combination of extra- and intra-oocytic yolk production. Therefore, all previous steps called "previtellogenesis" and "primary vitellogenesis" by Dhainaut and De Leersnyder [1], as well as Charniaux-Cotton [2, 3] and Zerbib [4] can be grouped into a previtellogenic phase. Moreover, it is necessary to be aware that the term "maturation" often found in aquaculture publications with the meaning of "ovarian growth" must be avoided for it corresponds to the resumption of meiosis following vitellogenesis (cf. Section III).

I. EARLY STEPS OF OOGENESIS AND PREVITELLOGENESIS

A. Chronology and cytology

The early steps of malacostracan oocyte growth were chiefly studied in the amphipod *Orchestia gammarella* and in few decapods from ultrastructural observations [1, 2, 4, 5; reviews in 3, 6, 7].

The undifferentiated gonad of young genetic females forms the germinative zone of the ovary. This structure that resembles a network in which each gonium is completely surrounded by mesodermal cells [8] persists the whole life of the female. Oogonial mitoses take place exclusively in the germinative zone [9].

In gonochoristic decapods, differentiation of the ovary is characterized by a precocious functioning of the germinative zone, i.e., by a precocious initiation of oogenesis as compared with spermatogenesis. Therefore, in the European crayfish, *Pontastacus leptodactylus leptodactylus,* oogenesis begins during the third postembryonic stage, while at the seventh stage the testes contain gonia not yet engaged in spermatogenesis. A similar delay between male and female gametogenesis also occurs in crabs and in the penaeid shrimp *Penaeus japonicus* [10–12].

In Talitridae amphipods, there seems to be a slight precocity in oogenesis in comparison with spermatogenesis. Such a precocity is clearly visible in males whose testes display an ovarian region.

Some oogonia leave *continually* the germinative zone [13] by a mechanism as yet unknown and rapidly enter prophase of the first meiotic division up to diakinesis. Then, they become primary oocytes with condensed chromosomes which appear in synaptonemal complexes at the ultrastructural level. The decondensation of chromosomes is accompanied by marked cytoplasmic changes such as an accumulation of free ribosomes and the differentiation of a rough endoplasmic reticulum (RER). These phenomena characterize the beginning of the previtellogenesis. Mesodermal tissue forms around each oocyte a follicle multilayered epithelium. Follicle cells are

connected with one another by desmosome-like cell junctions and are themselves holded by hemidesmosomes on the *basal lamina* [14]. When endogenous glycoproteins accumulate in the numerous RER vesicles, oocytes carry out the "endogenous vitellogenesis" [1]. Simultaneously, the oocytes acquire a vitelline envelope and their surface becomes irregular with the formation of short microvilli and a few micropinocytotic vesicles. Oocytes grow continuously until they reach a diameter typical for the species. Oogenesis stops at the end of this step in young females and during genital rest in puberal females [15, 16]. As a general rule, female genital puberty is realized when a one layered-epithelium surrounds for the first time each fully grown previtellogenic oocyte (cf. Section II, A).

B. Regulation

1. *Mechanisms of oocyte differentiation and onset of oogenesis*

The hypothesis of a spontaneous ovarian differentiation, or ovarian autodifferentiation, of the gonadal rudiment in the absence of diffusing androgenic hormone (AH) was stated for the first time by Charniaux-Cotton [17]. This hypothesis was based on the observation of a precocious development of an anterior ovarian region before the onset of spermatogenesis in the gonads of males of *Orchestia mediterranea,* Talitridae amphipods (rudimentary hermaphroditism). Gonia of the anterior region are less subjected to the AH – the androgenic glands (AG) are located posteriorly – and differentiate into oocytes that acquire follicle cells and grow until the end of previtellogenesis. Posteriorly to this region, gonia give rise to the various stages of spermatogenesis. Experimental proofs of an ovarian autodifferentiation in amphipods were then obtained in *O. montagui* after ablation of the AG by Charniaux-Cotton and Ginsburger-Vogel [18] and in *Talitrus saltator* after implantation of testes into males of *O. gammarella* from which AG have been removed [19]. In *O. gammarella,* the transformation of testes into ovaries is possible if the testes are protected from the action of AH, before the onset of spermatogenesis that occurs at the second intermolt. This is accomplished by implantation of gonads from young males into females. If implanted before the beginning of spermatogenesis, the young testes can develop into ovaries; if implanted later, the testes do not transform but instead degenerate [20].

Ovarian autodifferentiation has been also demonstrated in the oniscoid isopod *Helleria brevicornis* following implantation of undifferentiated gonads deprived of AG rudiments [21].

Among decapods, the proterandric hermaphroditic shrimps, such as *Pandalus borealis* and *Lysmata seticaudata,* give a good proof of the ovarian autodifferentiation (review in [22]). Thus, when the AG degenerate at the time of sex-reversal, or after their ablation (andrectomy) during the male phase, oogenesis spreads into the gonad. Another proof of ovarian autodifferentiation has been obtained in the shrimp *Macrobrachium rosenbergii* [23]. In young males in which the gonads contain only gonia, andrectomy is followed by differentiation of normal ovaries with oocytes in previtellogenesis and development of oviduct rudiments.

Several natural data confirm the inherent tendency of gonia in genetic females or males to effect oogenesis. Thus, female gametogenesis appears not only in the gonad rudiment of young males of several Talitridae, as *O. mediterranea* and *O. cavimana* [24], but also in the testes of mature males of gonochoristic decapods. For instance, the testes of the crayfish *Pontastacus leptodactylus leptodactylus,* exhibit oogenesis of variable intensity during genital rest. At this time, when the AG are very small, spermatogenesis stops and oocytes sometimes appear in different parts of the testes [11]. Thus, oogenesis may occur in some testicular acini as soon as the gonia receive an insufficient quantity of AH, or none at all. It results in the formation of normal primary follicles but this oogenesis always stops at the end of previtellogenesis (cf. Section II, B, 3, a).

To summarize, ovarian differentiation of the gonadal rudiment is an autodifferentiation. It concerns oogenesis from gonia to the end of previtellogenesis and takes place spontaneously in the absence of any hormone, female or male. This

proves the "emerging inherent tendency to develop into an ovary" as in mammals ([25], p. 39).

Initiation of oogenesis does not appear to be controlled by a neurohormone. In crabs, it is not accelerated by removal of eyestalks from larvae and from very young females, whereas a neurohormone from eyestalks regulates the initiation of spermatogenesis, through its moderating control of the AG [26, 27].

2. *Maintenance of the germinative zone*

The germinative zone of the ovary, in contrast to that of the testis, does not require the presence of a neurohormone for its maintenance. Thus, in the shrimps *Palaemon serratus* and *Crangon crangon*, after cauterization of the median zone of the protocerebron or culture of isolated ovaries, the gametogenic activity of the germinative zone persists [28–30]. Likewise, sacculinid rhizocephalans, through contact and at some distance, cause the destruction of neurosecretory regions of the host crabs in both sexes. However, the germinative zone of parasitized female crabs is not modified, while the one of parasitized males degenerates [31, 32].

3. *Oocyte growth until vitellogenesis*

As already mentioned, oogenesis up to the end of previtellogenesis is a continuous phenomenon. Some studies have shown that the continuous phase of oogenesis is regulated by a moderating neurohormone. In the juvenile freshwater crab *Eriocheir sinensis*, ablation of the eyestalks brings on an increase in the synthesis of DNA in the germinal cells that is expressed by an increase in the number of oogonial mitoses and in the number of oocytes entering into prophase of meiosis [33]. Molting hormone interferes little in oogonial mitoses and in previtellogenesis, as is shown by the ablation of Y-organs from the juvenile and prepuberal crabs [34]. Thus, small quantities of ecdysone which remain in serum after the ablation seem sufficient to allow a normal oogenesis in these destalked crabs.

On the other hand, when Y-organ and eyestalks are removed simultaneously, most of the previtellogenic oocytes degenerate. It appears that repeated injections of 20 OH-ecdysone are necessary to restore a normal previtellogenic growth in the destalked crabs [34].

Ablation of eyestalks in 1-year-old female *Paratelphusa hydrodromous*, during their postoviposition period, seems to accelerate previtellogenesis, leading to an early vitellogenesis. At that time, the ovaries normally show empty follicles. This result is given as an argument in favor of an inhibitory control of previtellogenesis by eyestalks [35].

The protein synthesizing capacity of previtellogenic ovaries of *Uca pugilator* has been tested for 24 hr *in vitro*. In presence of neuroendocrine tissues such as eyestalk or thoracic ganglion, as well as cyclic AMP (10^{-6} M), the rate of incorporation of radioactive leucine into protein by the ovary is inhibited [36]. Since cyclic AMP appears to mimic eyestalk tissue (well-known to have an inhibitory effect on oocyte growth, as recalled in Section II, B, 1), the decrease in protein sythesis is attributed by the authors to "changes in cyclic nucleotide levels". No clear interpretation concerns the inhibitory effect of the thoracic ganglion. The lack of a specific component from the medium would explain this unexpected effect occurring instead of the stimulation observed *in vivo*.

II. VITELLOGENESIS

A. Vitellogenesis process

1. *General considerations*

Vitellogenesis is the step of the crustacean reproduction during which oocytes accumulate a large amount of yolk, especially – but perhaps not exclusively – by internalization of an extraovarian precursor named vitellogenin. It affects synchronously all the elder oocytes, i.e., all the oocytes which have reached the end of previtellogenesis. Such a process is common to many groups other than Crustacea particularly in insects, amphibians, fishes and birds. From several aspects, vitellogenesis is a very important step of the female reproduction:

—Most of the endocrine controls on reproduction known at the present time apply on vitellogenesis.

—Contrary to previtellogenesis, vitellogenesis is

not a continuous process: it is inhibited during non-breeding season and, for some species, in artificial conditions. So, it is easy to understand that the aquaculture services play a special attention to the control of vitellogenesis mechanisms.

—The ability to carry out vitellogenesis is the criterium on which the puberty concept was built in female crustaceans.

Crustacean vitellogenin is a high molecular weight protein associated with lipidic, glucidic and carotenoid prosthetic groups to which very few studies have been devoted.

When vitellogenesis takes place, the presence of carotenoids linked to vitellogenin brings on a bright color of the ovary in most species. So, it is quite easy to know, without dissecting the animals, whether vitellogenesis has begun in the species whose exoskeleton is transparent, such as most prawns and shrimps.

2. *Origin of vitellogenin*

The existence in the haemolymph of vitellogenic females of a "female-specific-protein" – the early name for vitellogenin when the physiological significance of this protein was not firmly stated – was reported for the first time in Crustacea by Frentz [37] in the crab *Carcinus maenas.* This observation and the role of vitellogenin in the vitellogenesis process as the major precursor of yolk was confirmed in several other species during the following years [38–43 for review].

The site of vitellogenin synthesis in Crustacea was known quite lately and the question is not yet completely elucidated. The first hypotheses concerned the hepatopancreas [44] and were supported by the early observations on the transit of carotenoid pigments from this organ to the ovaries (e.g., [45]). However, nothing suggested that the proteinic part of vitellogenin has the same origin than the carotenes associated with it.

Kerr [46] cultured different tissues and organs from the crab *Callinectes sapidus* – muscle, heart, hepatopancreas, total haemolymph and serum – in the presence of ^{14}C-leucine and analyzed the protein released in the medium by column chromatography and electrophoresis. The author found some suggestion for the hemocytes as site of vitellogenin synthesis but the results did not seem conclusive.

In *Uca pugilator* and *Libinia emarginata* Wolin *et al.* [47] reported a complete immunochemical identity between vitellogenin and a protein from the hepatopancreatic extract. Nevertheless, haemolymph could have contaminated the extract. Recently, Paulus and Laufer [48], using immunohistochemical technics for the study of the crabs *Libinia emarginata* and *Carcinus maenas,* localized vitellogenin in hepatopancreatic specialized cells they called vitellogenocytes. According to the authors, these cells are contained in small haemal sinuses between the hepatopancreatic tubules and can be found in association with some other tissues, especially connective tissue. They may be similar to the adipocytes which are considered by other authors as the site of vitellogenin synthesis ([63], see further).

Lui *et al.* [49–51] incubated ovaries of the crayfish *Procambarus* sp. and of the crab *Pachygrapsus crassipes* in a ^{3}H-leucine medium or a mixture of tritiated amino acids up to 48 hr. After denaturation and electrophoresis, they demonstrated that radioactivity was present in the main polypetide subunits of *Procambarus* vitellogenin and in all the three subunits of that of *Pachygrapsus*; so they concluded that the ovaries are the source of vitellogenin. Unfortunately, the authors have not cultured other organs than ovaries as controls. Using similar methods to those of Lui *et al.,* Eastman-Reks and Fingerman [52] drawn the same conclusion about the ovary of the crab *Uca pugilator.* As the preceeding authors, they did not attempt to incubate other tissues. In the kuruma prawn, *Penaeus japonicus,* Yano and Chinzei [53] reported also that "ovary is the site of vitellogenin synthesis". These authors incubated ovaries and hepatopancreas – but no fat body – in Ringer solution containing labeled amino acids. Protein synthesized by the ovary and precipitated with anti-vitellin serum was shown by electrophoresis and fluorography to consist of two polypeptides corresponding to the components of vitellogenin. No immunoreactive material was found in the hepatopancreas and its incubation medium.

Some ultrastructural studies of the vitellogenic oocyte gave indications in favor of both intra- and extraoocytic sources of yolk (in the spider crab,

Libinia emarginata, the isopod, *Oniscus asellus,* the terrestrial hermit crab, *Coenobita clypeatus,* [54–56]).

In an amphipod Crustacea, *Orchestia gammarella,* Junéra *et al.* [57] showed that vitellogenin synthesis did not stop immediately after bilateral ovarietomy, as would be the case if the ovaries were the site – or, more precisely, the exclusive site – of vitellogenin synthesis: it only stopped 5 to 8 days after the operation for reasons which will be discussed further on (cf. Section II, B, 2, b). In 1980, Picaud and Souty using double diffusion technique and autoradiography, demonstrated that fat body from *Porcellio dilatatus* incubated with a ^{14}C-leucine medium synthesized vitellogenin. Junéra and Croisille [58] and Croisille and Junéra [59] made the same inference in *O. gammarella* but, in this species, the *subepidermal* adipose tissue only seems to be involved in vitellogenin synthesis. In the shrimp *Palaemon serratus,* Meusy *et al.* [60] demonstrated also by immunohistochemistry the presence of vitellogenin in the same structures of the vitellogenic females; the hepatopancreas was not labeled. Similar results were obtained later in two other decapods, the penaeids *Penaeus japonicus* [61] and *Parapenaeus longirostris* [62].

The adipocytes from *O. gammarella* display ultrastructural modifications when vitellogenin synthesis takes place [63]. They acquire a well-developed rough endoplasmic reticulum, the space in the cell occupied by β-glycogen and lipid droplets significantly reduces and the vitellogenin is detectable in dense bodies by the peroxidase-antiperoxidase method. Furthermore, when vitellogenin synthesis stops following a total ovariectomy, the adipocytes acquire the ultrastructural features of non-vitellogenic or male adipocytes [64].

Though some of these studies are seemingly contradictory, it should be noted that, in some insects – *Drosophila* and few others –, not only fat body but also follicle cells of the ovary are able to synthesize vitellogenin [65–67]; such a possibility of a double origin of vitellogenic material may exist also in Crustacea or in *some orders* of Crustacea. Moreover, the results about "vitellogenocytes" associated with the hepatopancreas [48] and those about "adipocytes" may not be inconsistent, since these two cellular types would be homologous. Incubation of fat body, ovary and hepatopancreas is a very hazardous method since the maintenance of the integrity of these tissues/organs during the process is not reliable. Particularly with the hepatopancreas, the release of proteolytic enzymes into the incubation medium is difficult to avoid. So, an attractive approach of this problem would be to look for messenger RNA coding for vitellogenin in these various tissues/organs.

3. *Vitellogenin uptake by vitellogenic ovaries*

a) Transformations and role of the follicle envelope

At the onset of vitellogenesis, each oocyte is surrounded by a follicle envelope which comes from a *permanent* tissue: the follicle tissue from the eggs which have been laid is utilized again for setting up the new follicles [3, 68–71], except in the isopod, *Idotea balthica basteri,* in which it seems to degenerate just prior to oviposition [72]. At the beginning of vitellogenesis, a tubular network has been observed in the cells of the follicle envelope of four species of Palaemonidae (*Palaemon adspersus, Macrobrachium rosenbergii* [70, 73, 74], *Palaemonetes varians* and *Palaemon serratus* (Jugan, unpublished)). These tubules, characterized by a diameter of 0.15 μm, are bound by a single membrane and enclose a granular electron-dense material. They connect up all the extracellular compartments: haemolymph, intercellular spaces, space between the oocytes and the follicle epithelium. After incubation of ovaries in a peroxidase containing medium, the diaminobenzidine reaction product was seen in the tubular network and in all these compartments. Peroxidase penetrated also into the vitelline membrane and in some pinocytotic vesicles of the oocytes [73, 74]. The tubular network regresses at the end of vitellogenesis [70, 75]. This structure which has been also described in copepods [76], makes easier the passage of substances from haemolymph to vitellogenic oocytes.

In *Idotea balthica basteri,* where no tubular network has been described, some features seem to play the same role as in Palaemonidae shrimps:

the cells of the follicle envelope acquire oocyte oriented villi, tight junctions appear between follicle villi and oocyte microvilli, and the spaces between follicle cells become very wide [72].

Beside its role of interface, the follicle envelope has an endocrine function. Charniaux-Cotton [77, 78] has demonstrated in females of *O. gammarella* that the vitellogenic ovary controls a secondary sexual characteristic which is temporary and appears during vitellogenesis: the long ovigerous setae on oostegites, the role of which is connected with incubation. The follicle cells are presumably the source of this ovarian hormone, though this has not yet been established (cf. Section VII, B, 1 and 2).

b) Vitellogenic oocyte and endocytosis mechanism

At the beginning of vitellogenesis, microvilli develop towards the follicle cells [54, 55, 79, 80]. In *M. rosenbergii,* some of them have been described penetrating deeply in tubules of the follicle cells [73, 74]. A glycocalyx, or cell coat, covers the external surface of the microvilli. In addition to microvilli, macrovilli have been also observed in an amphipod, *O. gammarella* [80] and in some decapods ([81]; *Lysmata seticaudata,* Zerbib, unpublished). These micro- and macrovilli increase considerably the oocyte surface and probably its exchange ability.

Endocytotic vesicles, 100–140 nm in diameter, appearing at the surface of the cortical ooplasm, have been described in many species. In some of them, their content seems to be drained towards yolk spheres by a network of microcanalicules, 45–60 nm in diameter in *Orchestia gammarella* (Fig. 1) and in the crayfishes *Astacus astacus* and *A. leptodactylus,* [4, 81]. It has been demonstrated, by incubating oocytes in a horseradish-peroxidase containing medium [82, 83] or by using fluoresceine isothiocyanate conjugated vitellogenin [47] or tritiated vitellogenin [378], that these structures are related to an endocytotic – and not exocytotic – process. Recently, Jugan and Soyez [84] conjugated vitellin of *Macrobrachium rosenbergii* with colloidal gold and observed a labelling at the surface of the microvilli, on endocytotic vesicles and yolk spheres. Jugan [75], working on *M. rosenbergii* demonstrated that vitellogenin internalization in Crustacea is a receptor mediated process. The receptors have a high affinity ($K_D = 3.5 \times 10^{-8}$) and are very numerous (about 10^{10} receptors per oocyte).

The yolk spheres grow in size by fusing together and are pushed towards the medullar ooplasm by those more recently formed. At the end of vitellogenesis, they take a polyhedric shape and measure up to about 40 μm ("yolk platelets"). It has been shown that yolk spheres contain a lipo-glyco-carotenoproteic material. Lipid droplets have been also observed during vitellogenesis, but the origin of their content still remains undetermined (cf. comments in: [6], pp. 472–473). The proteins and lipids represent the major enrichment of the ovaries during vitellogenesis ([85] cited in [6]).

The sequestration of vitellogenin by the oocytes is a *specific* feature of vitellogenesis. Nevertheless, a rough endoplasmic reticulum is still present during this phase and it seems likely that intraoocyte synthesis of proteinaceous material continues [4, 86–88]. Moreover, transfer of nuclear material to the ooplasm, as a possible prelude to protein synthesis, has been reported [89, 90]. As suggested by Adiyodi and Subramoniam [6], the relative emphasis on autosynthesis and heterosynthesis probably varies with species.

Some time *before* the end of vitellogenesis, microvilli (and also macrovilli in the species where they are present) regress and the endocytotic phenomena disappear (in the isopod *Idotea balthica,* [72] and in *M. rosenbergii,* (Jugan, personal communication)). The oocytes are overloaded with yolk spheres and lipid droplets, except in the cortical and perinuclear ooplasm. Cortical vesicles appear and seem to be related to the formation of the fertilization envelope (in *O. gammarella* [91]). For Goudeau and Lachaise working on *Carcinus maenas* [92], these cortical granules would originate from the "endogenous yolk" (cf. Section V, C).

4. *From vitellogenin to vitellin: a processing?*

When vitellogenin, previously termed "female specific protein", enters the oocytes, it is usually named vitellin (or lipovitellin). With a historical regard, it seems that these two different names

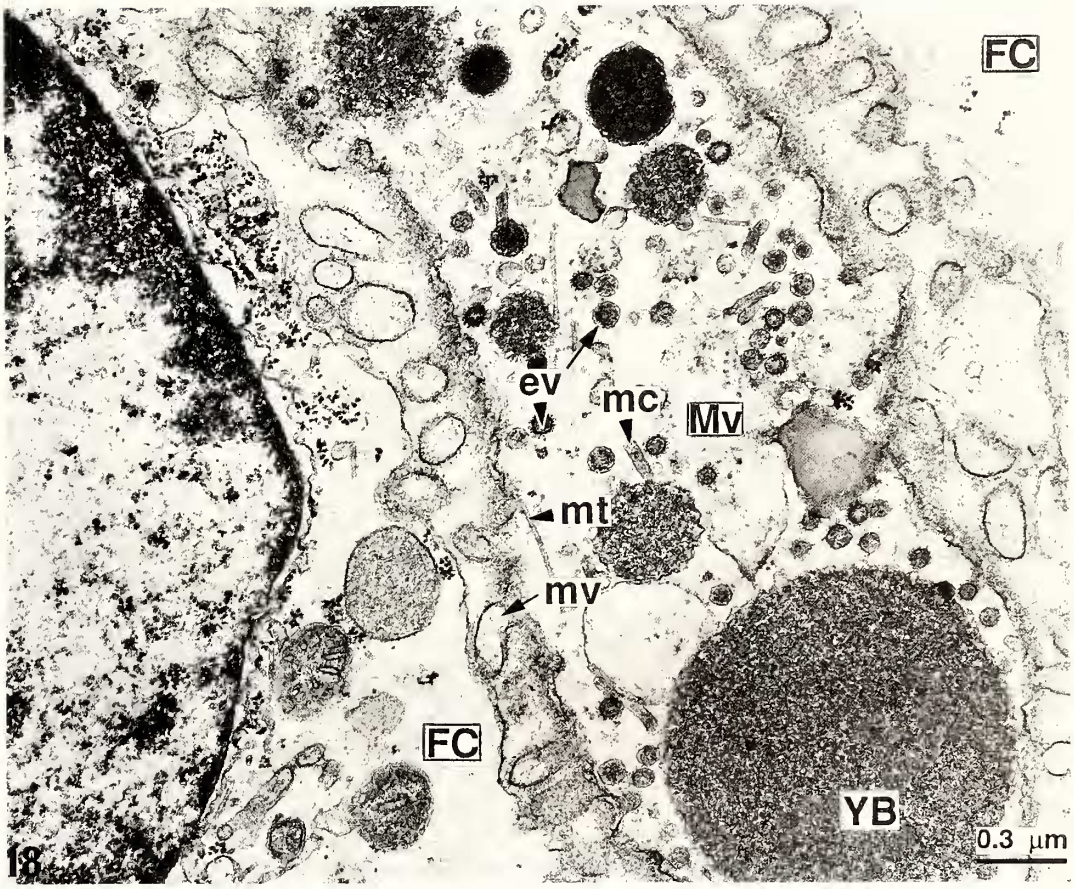

FIG. 1. Active endocytosis during vitellogenesis in the amphipod, *Orchestia gammarella*, and relationship between the oocyte and the follicle cells (FC) (courtesy of C. Zerbib).
ev: endocytotic vesicles; FC: follicle cells; mc: microcanalicules; mt: microtubules; Mv: macrovilli; mv: microvilli; YB: yolk body.

referred principally to the two compartments, haemolymph and oocytes, where these substances were found. Little was known about the chemical structure of vitellogenin and vitellin respectively.

The "female specific protein" of the haemolymph, i.e., vitellogenin, was initially characterized as an electrophoretically slow moving protein [37]. In the following years, the relation of vitellogenin to vitellogenesis was firmly established (cf. for review [93]). The presence of associated lipids (Sudan Black staining), carbohydrates (PAS positiveness) and carotenoids (pigment extraction and absorption spectrum study) was demonstrated and vitellogenin was consequently identified as a lipo-glyco-carotenoprotein (e.g., the early works: in the crabs *Paratelphusa hydrodromous* [39], *Carcinus maenas* [94] and *Callinectes sapidus* [42]). The carotenoids give a bright color – varying according to the species – to the vitellogenin and vitellin and, consequently, to the vitellogenic oocytes. They are provided by the food and are not synthesized by the animal itself. It seems probable that they have a screening function against light (review in [95]; [96]). The molecular weight (MW) of the vitellogenin in Crustacea was reported in the amphipod *O. gammarella*: 397 ± 27 kD [57], and in the isopod *Porcellio dilatatus*: 315 ± 54 kD [97].

Vitellin, the major constituant of yolk, is also a lipo-glyco-carotenoprotein. It contains between 28

and 35% of lipids [98, 99] and about 4.8% of sugars [100]. On the basis of double-diffusion tests or related techniques, no immunological difference between vitellogenin and vitellin has ever been demonstrated in any species [42, 47, 99, 101–106].

The MW of vitellin is not very different from that of vitellogenin in the species where both have been determined [57, 97, 107]. The amino acid composition of the vitellin of some species has been established ([50, 51, 99, 107–109]; the results are compared in the review [6]), but no comparison with vitellogenin is available; so, these data bring no indication on a possible processing. Treatment of the vitellin by denaturing agents revealed in several species the presence of two polypeptide subunits with close MW of about 100 kD (*Palaemon adspersus, Uca pugilator, Homarus gammarus, Macrobrachium rosenbergii* [52, 96, 110, 111]; *Penaeus japonicus*, MW not determined [53]) or less (*Parapenaeus longirostris,* 45 and 66 kD, [106]). In the prawn, *Macrobrachium rosenbergii,* the vitellogenin and the vitellin have been both studied and exhibited the same two subunits of 84 and 92.2 kD MW [111]. In some other species, numerous fractions have been visualized (*O. gammarella, Procambarus* sp., *Squilla mantis, Penaeus japonicus* [50, 107, 112–114], but it seems probable that only few of them are native polypeptide subunits.

Although the possibility of a processing of the vitellogenin when, or after, entering the oocytes has been considered, especially with regard to the proteinic part of this yolk precursor, few informations are yet available. It is likely that vitellogenin and vitellin, if not identical, are very closely related substances.

5. *Vitellogenin synthesis and vitellogenin level in haemolymph as means for monitoring vitellogenesis*

A first attempt to know whether there is a close relation between the vitellogenesis process and the vitellogenin metabolism was carried out by injecting tritiated leucine to vitellogenic females of *Orchestia gammarella* at various steps of the reproductive cycle [115, 116]. The diagram (Fig. 2a) shows that the amount of radiolabeled vitellogenin in the haemolymph is growing from the beginning to the 3/4 of the cycle, though endocytosis is maximal during this period (except at the very beginning of the cycle). This amount falls down during the last quarter of the cycle, though endocytosis, as seen by electron microscopy in several species (*Idotea balthica basteri* [72], *Palaemonetes varians* and *Macrobrachium rosenbergii* (Soyez and Jugan, personal communication)), become negligible at this period.

This result has been confirmed by *in vitro* incorporation of ^{14}C-leucine by the fat body of an isopod, *Idothea balthica basteri* (Fig. 2b)[117]. In addition to this statement, a diurnal rhythm of vitellogenin release was observed *in vivo* in another isopod, *Porcellio dilatatus* [118]. Other haemolymphatic and ovarian proteins seem also to be subjected to circadian variations [119–121].

In the lobster, *Homarus americanus,* where the reproductive cycle is not easy to study because it lasts about one year or more, it has been shown that the level of circulating vitellogenin, as measured by electrophoregram scanning, "is always highest well prior the maximum accumulation of yolk in the oocytes, and the levels dropped off markedly prior to oviposition" [105].

In the freshwater prawn, *Macrobrachium rosenbergii,* whose reproductive and molting cycles are short (about 3 weeks) and concomitant, as those of *O. gammarella,* an ELISA titration of circulating vitellogenin has shown that the vitellogenin level, very low at stages A and B, increases during stage C, i.e., during the period of intense uptake of vitellogenin by the oocytes, remains at a high level during stages D_0–$D_{1'}$ and fall down thereafter, though vitellogenesis is not still achieved (Fig. 3) ([111]; Derelle and Meusy, unpublished data). At the end of the molting/reproductive cycles, before and just after exuviation, the vitellogenin level is very low again. It will go up after oviposition if a new vitellogenesis takes place again. It is noteworthy that during the period of rapid decrease of the vitellogenin level, the vitellogenic oocytes display no more endocytosis but, nevertheless, their vitellin content increases up to oviposition. This observation is an indication for a vitellin synthesis by the oocytes themselves.

These studies, carried out on various species, firmly established that vitellogenin synthesis and

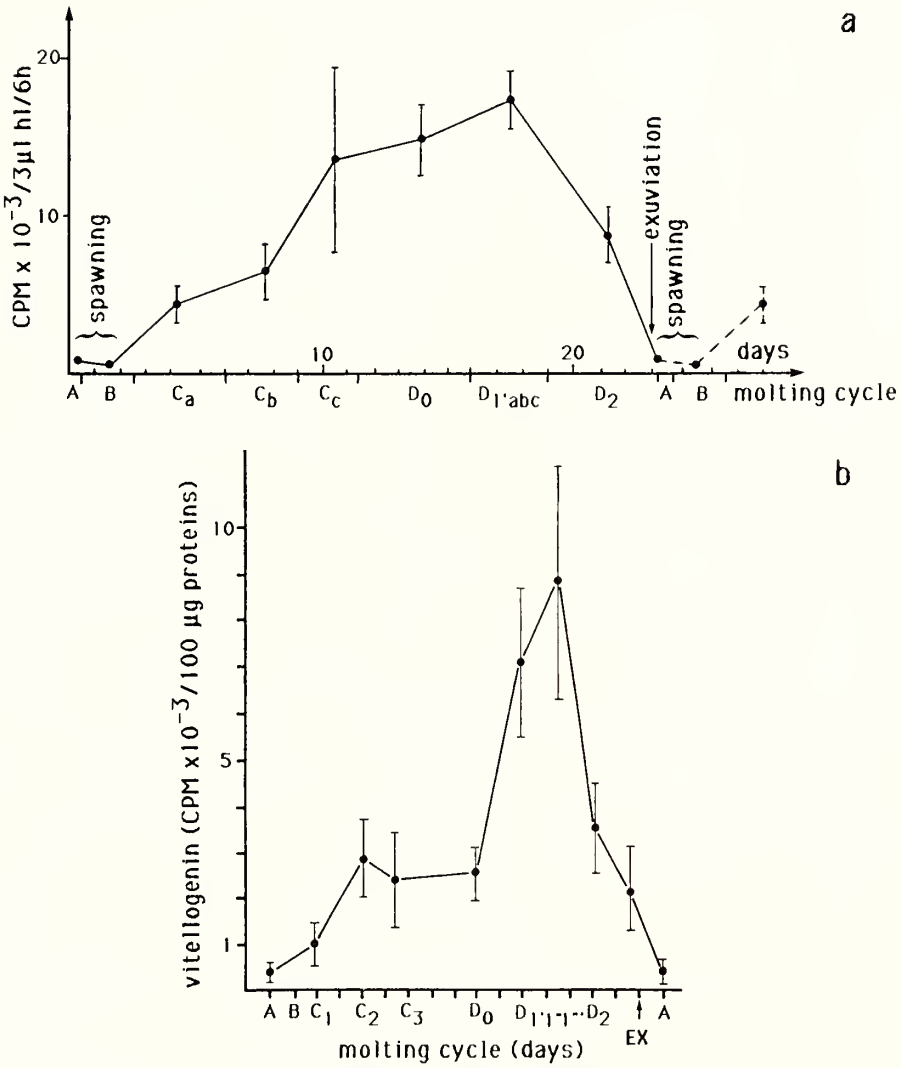

FIG. 2. (a) Vitellogenin synthesis in the amphipod, *Orchestia gammarella*, during the molting cycle.
Six hours before sampling of the haemolymph, the animals received an injection of 2.5 µCi of ^{3}H-leucine. The radioactivity of the vitellogenin was determined after separation by polyacrylamide gel electrophoresis of the serum proteins and corresponds to 3 µl of haemolymph (from [116, 347]).
(b) Relationship between the incorporation rates of ^{14}C-leucine by incubated fat bodies and the ovarian cycle (or molting cycle) of the isopod, *Idotea balthica basteri* (from [117]).
EX: exuviation.

vitellogenesis are closely correlated. Some important aspects of the mechanisms of control begin now to be elucidated.

6. *Timing of the reproductive cycle: duration and relation with the molting cycle*

The duration of the female reproductive cycle in malacostracan Crustacea generally reduces when temperature increases and is very different from one species to another. For instance, it lasts about 3–4 weeks in the amphipod *Orchestia gammarella*, reared at the laboratory temperature, and in the prawn *Macrobrachium rosenbergii* at 27°C (observations made in our laboratory), several

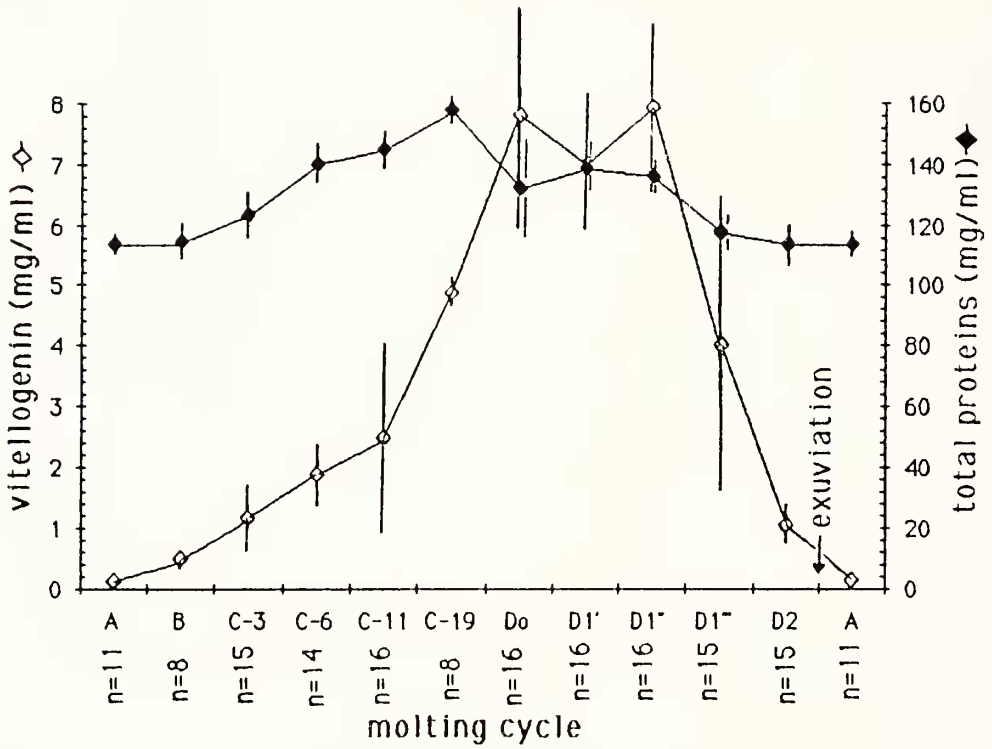

FIG. 3. Variations of circulating vitellogenin and total protein titres during the molting cycle in vitellogenic female prawns, *Macrobrachium rosenbergii*, of the same size.
The titres of vitellogenin were determined by indirect ELISA and total proteins by Lowry's method (Derelle and Meusy, unpublished data).
Bars: standard error of the mean; n: number of animals for each molting stage.

months in many species and about one or two years in the lobster, *Homarus americanus* [105, 122].

Various features can be found concerning the relation between vitellogenesis and molting cycle. In some species, vitellogenesis takes place during one intermolt and egg laying occurs just after the exuviation (for instance, in the amphipod, *O. gammarella* [123], the isopods, *Porcellio dilatatus* and *Idotea balthica* [124, 125], the decapods, *Lysmata seticaudata* and *M. rosenbergii* [16, 69]). In some other species, vitellogenesis can take place during more than one molting cycle, according to the season (for instance, in the decapods, *Palaemon serratus* and *Athyaephyra desmaresti* [126, 127]).

It is noteworthy that the molting cycle generally lasts a longer time during the reproductive season than during the genital resting period, because vitellogenesis lengthens the cycle [123, 126].

In all these above malacostracans, egg laying takes place just after the exuviation. This is not the case of the crab, *Carcinus maenas*, whose vitellogenesis occurs only during the intermolt stage C_4 and which lays its eggs before premolt stages (D_0 to D_2), i.e., a long time before the exuviation [128]. In the crab, *Uca pugilator*, Webb [129] gives the following sequence of events: vitellogenesis – oviposition – incubation – hatching – molt. In the stone crab, *Menippe mercenaria*, several spawnings may occur within a single intermolt [130].

A very particular feature is that of few malacostracans which do not molt their whole life and become pubescent after their last molt, called "puberty molt" (cf. Section II, B, 2, d). In conclusion, the relationship between vitellogenesis and molting exhibits in Crustacea many different

features and seems to have supported a long and divergent evolution.

B. Vitellogenesis control

1. *Inhibitory control by VIH (Vitellogenesis Inhibiting Hormone)*

The first control to be known was inhibitory and its source is located in the central nervous system (cf. Fig. 4 for schematic representation of the main endocrine controls of vitellogenesis).

a) The X organ-sinus gland complex

Eyestalked species The works of Hanström, who discovered neurosecretory cells in the eyestalks of some species of stomatopods and decapods – the X organ or "Hanström's organ" – and a connected neurohaemal organ – the sinus gland [131–133] –, marked the beginning of the modern studies on crustacean endocrinology. At this time, the concept of neurosecretory cells was new: it was brought out only few years ago by Ernst Scharrer [134] from the observation of the hypothalamo-hypophyseal complex in Teleostei.

X organ is contained in the *medulla terminalis* of the optic lobes (protocerebrum), and consists of perikarya whose axons end in the sinus gland. The sinus gland, opalescent looking, is not really a gland but a neurohaemal organ. It stores and releases by exocytosis materials mainly from the X organ and contains no cell, except glial cells ([135–138]; review in [139]).

The role of the X organ-sinus gland complex was demonstrated by Panouse [140, 141], in the shrimp *Palaemon serratus*. This author observed that eyestalk ablation induces an acceleration of the molting cycle and a rapid growth of the ovary. He did not specify what stage of oogenesis was

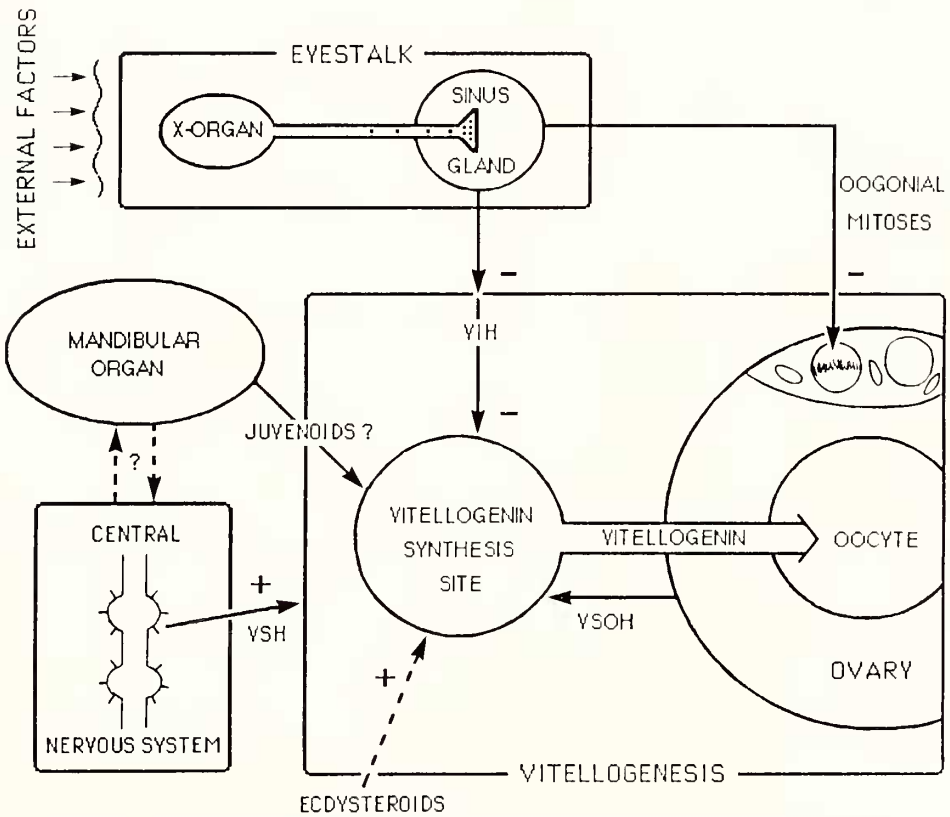

FIG. 4. Schematic representation of the main endocrine controls of oogenesis in malacostracans.
VIH: vitellogenesis inhibiting hormone; VSH: vitellogenesis stimulating hormone; VSOH: vitellogenin stimulating ovarian hormone.

specially affected by this ablation and he thought that the two effects, on molting and ovogenesis, could result from the suppression of the same hormone ("anti-auxinic effect of the eyestalk hormone"). The results of Panouse's experiments, classically referred as "the Panouse effect", found their applying in aquaculture. In some species, the breeders do not carry out vitellogenesis in artificial conditions: a unilateral eyestalk ablation is usually practiced to trigger vitellogenesis [142]. A bilateral ablation is not required and has some disadvantages varying with species: for instance, it may shorten the life of the female and/or bring about some abnormalities of vitellogenesis [143, 347].

An extensive bibliography of the early works on the anatomy and physiological functions of the X organ-sinus gland complex is given in the book of Gabe [144] and a more recent review has been produced by Chaigneau [139].

It is noteworthy that eyestalk ablation often promotes either vitellogenesis or molting, according to the species, state of the ovaries, age of the animals, and temperature. The idea arises of a molting-vitellogenesis antagonism, though the real mechanism of this antagonism, hormonal or metabolic, remained unknown [35, 145, 146]. This hypothesis was backed up by the observation of the females of some Oxynrhyncha which molt during a limited part of their life and whose reproduction begins after the last molt and the degeneration of the Y-organ (molt organ): *Pisa tetraodon, Libinia emarginata* [147, 148].

While many other hormonal effects of the X organ-sinus gland complex were discovered and studied, i.e., on glucidic and lipidic metabolism, water balance, and chromatophores, most of the authors thought that vitellogenesis and molting are controlled by two distinct hormones, the Molt Inhibiting Hormone, MIH [149], and the Ovary Inhibiting Hormone, OIH [150]. The early ultrastructural observations of the sinus gland were in agreement with the hypothesis of several hormones (for review [139]), though the typing of the neurosecretion granules only took into account morphological criteria. It is clear enough that the number of granule types cannot be directly related to the number of alleged hormones. It is now established that the "Ovary Inhibiting Hormone" acts mainly on vitellogenesis and is responsible for the sexual rest. So, the name of "Vitellogenesis Inhibiting Hormone" (VIH), proposed by Charniaux-Cotton and Touir [16], seems more adequate and precise.

Eyestalkless species The whitish and opalescent aspect of the sinus gland makes it quite easy to identify the gland in the vicinity of the optic lobes in eyestalkless species (review in [139]). In contrast, the identification of a structure homologous to X organ is much more difficult.

In the isopods which have no medulla terminalis, connections between neurosecretory cells of the brain and the sinus gland were found in *Porcellio dilatatus* [151], but the search for an X organ equivalent was mainly carried out by elective destruction of parts of the protocerebrum and optic lobes. Most authors located the source of VIH in the median part of protocerebrum (in *Idothea balthica* and *Ligia oceanica* [125, 152, 153]).

In the amphipod, *Orchestia gammarella,* electrocoagulation of the antero-median part of the protocerebrum prevents the onset of vitellogenesis and this zone can be considered as stimulatory [116]. A VIH or a VIH-like substance seems to be secreted by some other part of the brain: a supernumerary brain grafted into females of this species inhibits vitellogenesis [154]. According to the author, the graft, which is deprived of external influences, would secrete continously the inhibiting hormone. The concerned neurosecretory cells remain to be found in this order.

b) Ways of action

Control of vitellogenin synthesis When the concept of vitellogenin as the haemolymph precursor of vitellin became established, it appeared likely that the inhibitory action of VIH on vitellogenesis could act via the control of vitellogenin synthesis. Frentz [37] and Shade and Shivers [83] reported indications favorable to this hypothesis. Meusy *et al.* [60], injecting tritiated leucine to female shrimps, *Palaemon serratus,* showed that the ablation of eyestalks triggers vitellogenin synthesis. This result was confirmed and extended by *in vitro* experiments in the isopod, *Porcellio dilatatus:* extracts of sinus glands from non-vitellogenic females display a direct inhibitory

effect on vitellogenin synthesis by the fat tissue [155].

Control of vitellogenin uptake by the oocytes Unpublished observations on the amphipod, *O. gammarella,* by Meusy and Junéra suggested that the vitellogenin uptake might be hormonally controlled. Females do not usually lay eggs if mating has not occurred, for instance, in the absence of male. In this circumstance, a resorption of the non-laid oocytes is observed and, consequently, a very large amount of vitellin is detected in the haemolymph [101, 102]. Though vitellin could be used for a new vitellogenesis, in place of vitellogenin, as it has been proved by injecting radiolabeled vitellin in a vitellogenic female (Meusy, unpublished data), it happened that some of these females enter in the resting period, especially if the experiment was carried out at the end of autumn or at the beginning of winter. Similar observations were conducted on the prawn, *Macrobrachium rosenbergii,* when females were experimentally prevented from egg laying.

Direct evidence for a hormonal control of vitellogenin uptake by the oocytes of the prawn, *M. rosenbergii,* has been related by Jugan and Soyez [84]: a sinus gland extract inhibited the binding of colloidal-gold labeled vitellin on oocyte microvilli (Fig. 5). In preliminary studies using peroxidase-labeled vitellin, Jugan [75] reported that the affinity of VIH for the receptors to vitellin would be higher than that of the vitellin itself.

c) Extraction and purification of VIH

Though some other eyestalk hormones have been isolated in the seventies [156–158], the first attempt at purification of VIH was published only in 1981 by Bomirski *et al.* [159]. In a preliminary study, Klek-Kawinska and Bomirski [160] realized aqueous extracts of eyestalks of the shrimp, *Crangon crangon,* and tested their activity on destalked females of the same species. They found that the hormone is apparently absent during the early part of the breeding season. Later on, Bomirski *et al.* [159] dialysed, boiled and filtrated on Sephadex G–25 gel the eyestalk extracts from *Cancer magister* before testing them on destalked females of *Crangon crangon.* They concluded that VIH – they called GIH, i.e., Gonad Inhibiting Hormone –, is heat stable, dialyzable and has a molecular weight of about 2000 Daltons. The thermostability was confirmed in the spiny lobster, *Panulirus argus* [146]. Quackenbush and Herrnkind [161], after extraction in phosphate buffer, pH 6.8, separated VIH and other peptides from the eyestalks of the spiny lobster, using Sephadex G–25 gel and bioassayed the fractions in eyestalkless female fiddler crabs, *Uca pugilator.* According to these authors, this neuropeptide has an apparent molecular weight near 5 kD and is different from the Molt Inhibiting Hormone, MIH, which did not induce gonadal inhibition. In a recent abstract, Quackenbush and Keeley mentioned a lighter MW for the GIH–VIH of the shrimp *Penaeus vannamei*: 3.3 kD [162].

More recently, Soyez *et al.* [163] extracted proteic material from isolated sinus glands of the lobster, *Homarus americanus,* with 0.1 N hydrochloric acid and purified the active factor by a two step reversed phase high performance liquid chromatography procedure. A bioassay, operated on destalked females of the shrimp, *Palaemonetes varians,* and an SDS-urea polyacrylamide gel electrophoresis revealed the presence of a single active peptide with a molecular weight between 7 and 8 kD. Some other peptides of similar molecular weight and with closely related elution time were partially characterized. Their amino-acid composition exhibits broad similarities (Soyez *et al.,* unpublished data).

d) Latest data on VIH

Recently, Meusy *et al.* [164] demonstrated that VIH from the lobster, *H. americanus,* is not strictly species specific from immunochemical criteria: the antibodies raised against the purified VIH from *H. americanus* crossreact in direct ELISA with sinus gland extracts from some other species (shrimps: *Palaemonetes varians* and *Palaemon serratus*; prawn: *Macrobrachium rosenbergii*; crab: *Carcinus maenas*) and not with that from several others (prawns: *Penaeus vanamei* and *P. monodon*; crayfishes: *Astacus leptodactylus* and *Orconectes limosus*; spiny lobster: *Jasus paulensis*). Immunocytochemical studies of the sinus gland of *H. americanus,* using the same antibodies and colloidal gold labelling, revealed that VIH is mainly localized in electron dense granules of medium size, 110–185 nm in diameter (Fig. 6).

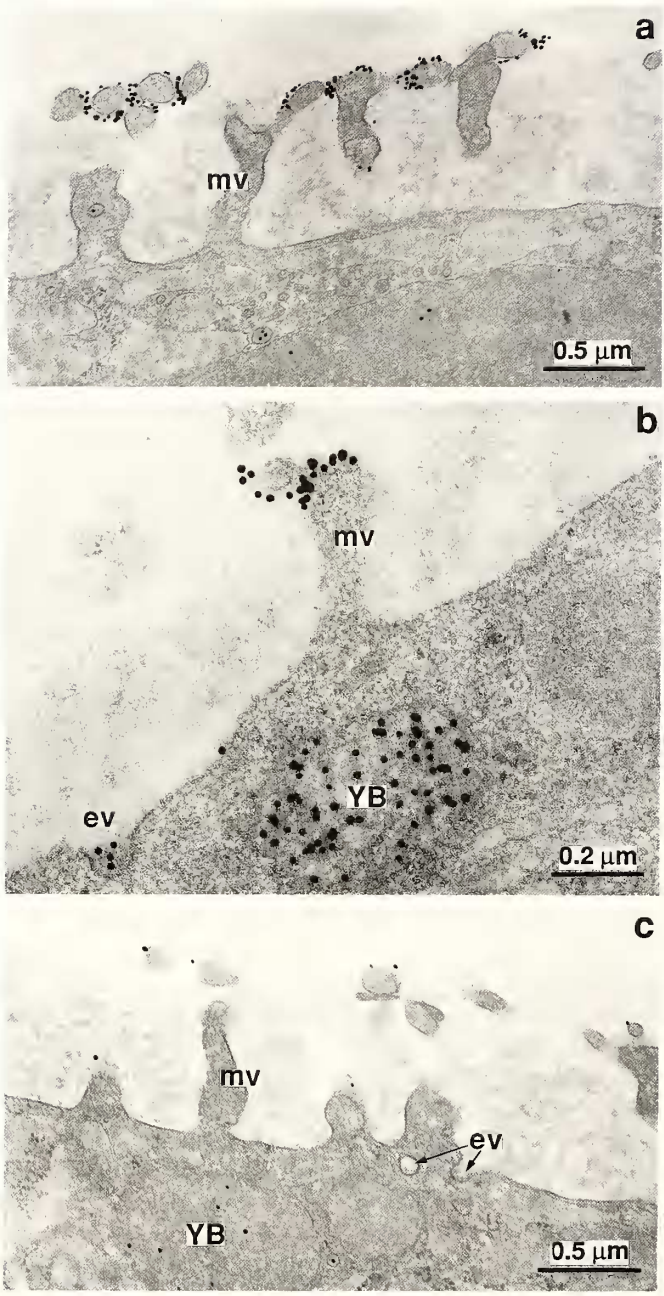

FIG. 5. Endocytosis in the prawn, *Macrobrachium rosenbergii*, as studied by incubation of vitellogenic oocytes in a medium containing colloidal gold conjugated vitellin (a, b). The effect on endocytosis of a sinus gland extract is shown (c).
Microvilli (mv), endocytotic vesicles (ev) and yolk bodies (YB) are labeled. No significant labeling is observed in the presence of a sinus gland extract (courtesy of P. Jugan and D. Soyez).

Similar studies with an antiserum raised against the Crustacean Hyperglycemic Hormone (CHH) [165] have shown that this hormone, chemically related to VIH, is contained chiefly in large granules (170–260 nm) (Meusy *et al.*, unpublished results). So, the axonal endings, and consequently the neurosecretory perykaria, seem specialized, though the number of granule types recognized is below that of the neurohormones yet known. It is likely that the criteria, mainly morphological, used for the typology of the secretory granules may not be satisfactory.

2. *Stimulatory control*

Many examples of hormonal antagonisms available in other groups, especially in mammals, suggested the possible occurrence of a vitellogenesis stimulating system in Crustacea. Moreover, following the opinion of some authors, the variable effect of eyestalk ablation on vitellogenesis, gener-

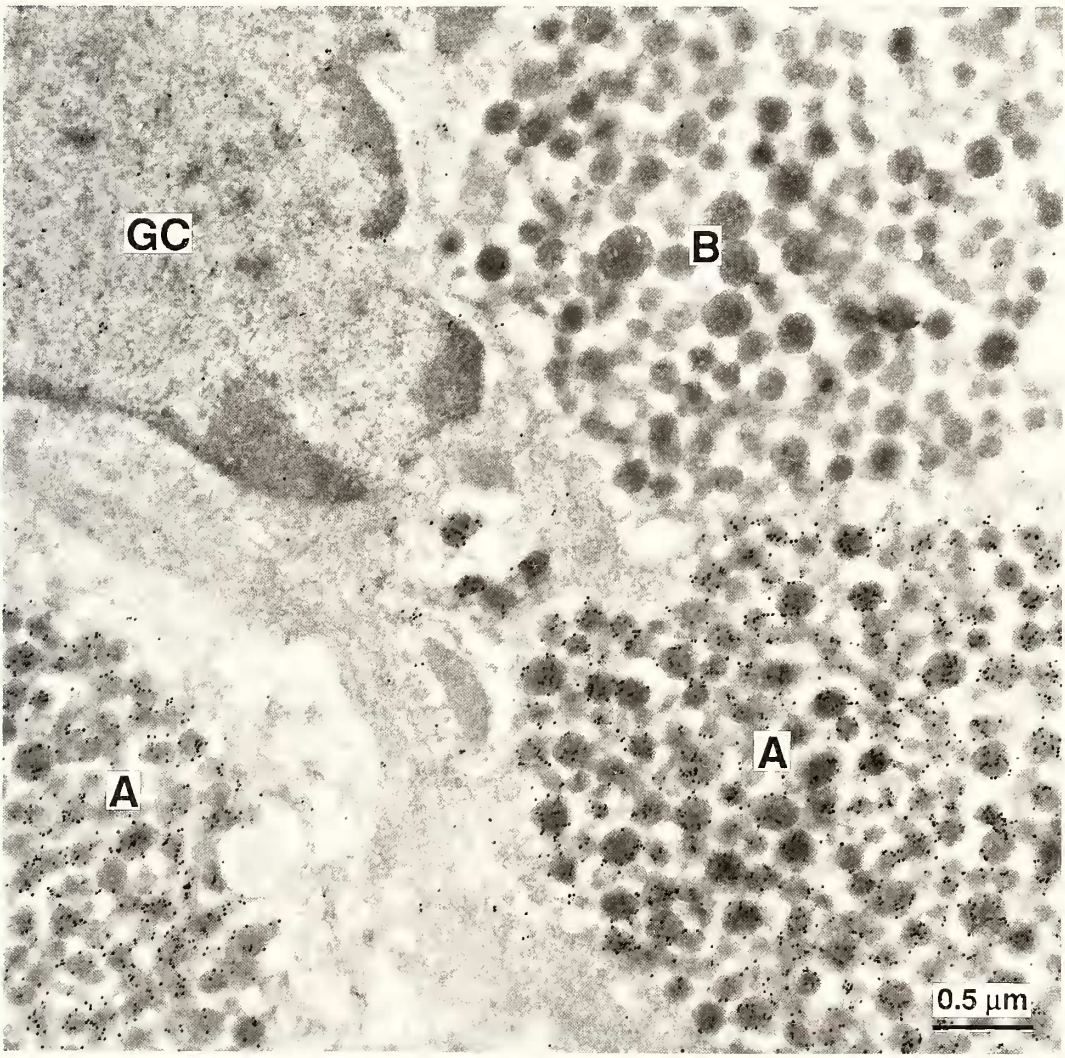

FIG. 6. Immunocytochemical (colloidal gold) staining of VIH in the sinus gland of the lobster, *Homarus americanus*, using a mouse serum against *H. americanus* VIH as primary antibody. The labeling is located on neurosecretory granules of medium size (A) (110–185 nm in diameter). The larger granules (B) (170–260 nm) are not labeled (from [164]).

ally stimulatory but dependent on the sexual condition of the female, the species and the environmental circumstances, seems to credit the hypothesis of an antagonistic control.

a) Neurohumoral factors

Though secretory cells have been described initially in the thoracic ganglia of crabs [166, 167], Otsu [168, 169] gave the first indications of a stimulatory control of vitellogenesis by substances issued from these structures: he observed a precocious development of the ovaries in the crab, *Potamon dehaani,* after implantation of thoracic ganglia. This result was confirmed in some other decapods [170–173].

Boiled aqueous extracts of thoracic ganglia from the fiddler crab, *Uca pugilator,* stimulated vitellogenesis in both intact and destalked crabs [36]. Takayanagi *et al.* [174] demonstrated *in vivo* and *in vitro* that aqueous extracts from not only thoracic ganglia but also brain have a positive effect on vitellogenesis in oocytes of the shrimp *Paratya compressa.* In the amphipod, *O. gammarella,* where the role of the thoracic ganglia has not been investigated until now, Blanchet-Tournier *et al.* [116] demonstrated that the antero-median part of the protocerebrum is stimulatory.

To conclude, the existence of an aqueous-soluble substance, secreted by nervous cells and having a stimulatory effect on vitellogenesis, seems established. However, the nature of this substance – perhaps a peptide –, its precise origin and the mechanism of its action remain to be studied.

b) Vitellogenin Stimulating Ovarian Hormone (VSOH)

As already mentioned (cf. Section I, B, 1), the ovary of Crustacea develops itself, i.e., its differentiation is not hormonally controlled [175, 176]. On the contrary, the testis – and the male secondary characters – are induced by the androgenic hormone secreted by the androgenic glands whose development is genetically induced [175].

If the testis is protected against the action of the androgenic hormone before the onset of spermatogenesis, it develops into an ovary (cf. Section I, B, 1). But the surgical suppression of the androgenic glands in *pubescent* males is generally followed by the arrest of spermatogenesis and the degeneration of the testes only: vitellogenin synthesis, as well as oogenesis, do not take place. It has been demonstrated in *O. gammarella* that the implantation of an ovary is necessary for triggering vitellogenin synthesis [177].

On the other hand, the ovariectomy in vitellogenic females of *O. gammarella* is followed by the arrest of vitellogenin synthesis [177] and the fat body acquires the same features as the fat body of males and non-vitellogenic females [64]. This effect, considered alone, could be eventually explained by a feed-back regulation mechanism, as suggested by Picaud and Souty [178] for similar results obtained in females of the isopod, *P. dilatatus.* But the results of the preceding experiments performed on males of *O. gammarella* plead in favor of an ovary hormone. It might be possible that VSOH is the same hormone as the ovarian hormone controlling the ovigerous setae ([77, 78]; cf. Section VII, B). In the isopod, *Armadillidium vulgare,* vitellogenin synthesis is not ovary dependent [179].

Up to now, no other study has been carried out on VSOH which seems to play a similar role to that of estradiol-17β in egg laying vertebrates.

c) Ecdysteroids

The Y-organs are responsible for molting [180] by secreting α-ecdysone, which is hydroxylated to the active hormone, 20 OH-ecdysone, also called β-ecdysone, ecdysterone or 20β-hydroxyecdysone [181–185, 345].

Except the early works [186–190], several studies have shown that vitellogenesis cannot take place after Y-ectomy in the isopods, *Idotea balthica, Porcellio dilatatus* and *Armadillidium vulgare* [125, 191, 193], and in the amphipod, *Orchestia gammarella* [192]. Nevertheless, the relationship between 20 OH-ecdysone secretion and vitellogenesis is not easy to define. It has been demonstrated by radioimmunoassay that a high peak of ecdysteroids occurs in the haemolymph of various species before exuviation, during a short time of stage D_2 (or D_2–D_4) of the molting cycle (in the crab *Carcinus maenas,* in *O. gammarella,* in the shrimp, *Palaemon serratus* [194–197] and in the prawn, *Macrobrachium rosenbergii,* Derelle and Meusy, unpublished data). Vitellogenesis and

vitellogenin synthesis have begun a long time before this short increase of ecdysteroid level in haemolymph and cannot be directly related to this phenomenon (Fig. 7a and 7b). Moreover, molting and reproduction cycles are not synchronous in several Crustacea. The extreme instance is that of oxyrhynch crabs whose Y-organs degenerate in males as well as in females and enter a terminal anecdysis after the puberty molt [198, 199].

Further data on the effect of molting hormone on vitellogenesis have been brought on by studies on vitellogenin. Meusy *et al.* [192] have demonstrated that Y-ectomy in *O. gammarella* is followed by a decrease of the vitellogenin synthesis. In the isopod, *Porcellio dilatatus* [200], a decrease of the amount of the circulating vitellogenin was observed after Y-ectomy and this effect has been compensated by 20 OH-ecdysone injection to the animals. But administration of 20 OH-ecdysone to *non-operated* females of *O. gammarella* failed to trigger or stimulate the vitellogenin synthesis [201]. Furthermore, molting hormone is not necessary for an *in vitro* synthesis of vitellogenin by the fat body from female [202] or even male *P. dilatatus* [203], though an *in vivo* stimulatory effect has been reported in this species [200]. A stimulatory effect has been also reported on ovarian protein synthesis [348].

So, it is unlikely that the molting hormone plays a *specific* stimulatory effect on the vitellogenin synthesis and the vitellogenesis. Numerous studies carried out on insects seem to credit 20 OH-ecdysone with a stimulatory effect on several metabolisms, but not specifically on the vitellogenin synthesis which is controlled by juvenile hormone (the haematophagic insects, where 20 OH-ecdysone triggers vitellogenin synthesis after a blood meal, seem to be a particular feature).

The function and destiny of the ecdysteroids found in the ovaries of *O. gammarella* at the end of the vitellogenesis [196] and in the ovaries of *Carcinus maenas*, especially ponasterone A [204, 205], are still undetermined.

d) Juvenoids

Some authors have speculated that the juvenile hormone, JH, which regulates metamorphosis and gametogenesis in insects might also play a role in the physiology of crustaceans. Four approaches to this topic were carried out by: 1) injecting juvenile hormone or analogs; 2) observing some structural similarities of the mandibular organs of Crustacea with the corpora allata of insects and steroid-producing cells; 3) implanting these mandibular organs in experimental animals; 4) identifying sesquiterpenoid compounds in haemolymph and mandibular organs.

Several authors have observed a chemosterilant effect of JH-I (on *Orchestia gammarella* [68]) or juvenile hormone analogs (on the mud crab, *Rhithropanopeus harrisii* [206], and on the immature spider crab, *Libinia emarginata* [207]). In these experiments, the addition of hormone increased the current haemolymphatic level to a supraphysiological state which might have toxic effects on the ovary. Similar results have been reported in insects ([208], p. 247), though the corpora allata, source of juvenile hormone in insects, are necessary for vitellogenin synthesis and vitellogenesis in most species [209].

The presence of corpora allata has never been pointed out in Crustacea but endocrine organs located in the vicinity of each mandible have been described by Le Roux [210] who postulated that these organs might have an endocrine function related to oogenesis. The ultrastructural features of the so-called mandibular organs showed analogies with steroid-producing cells [211–213] and corpora allata of insects [214].

The mandibular organs are controlled by the eyestalks, probably by a hormone from the sinus glands: they become hypertrophied after eyestalk ablation [211, 215]. Their involvement in vitellogenesis has been suggested in *Libinia emarginata*: mandibular organs from adult male spider crab were able to induce vitellogenesis when implanted in immature females [216].

After a preliminary work [217] in which the authors detected a juvenile hormone activity in two decapods, Laufer *et al.* [218] demonstrated the *in vitro* secretion of methylfarnesoate by the mandibular organs of *Libinia emarginata*. This compound is structurally and biologically related to JH-III, as a major product, and a very small amount of JH-III (1000 times less than methylfarnesoate). After eyestalk ablation, the secretion of methylfarnesoate was enhanced by at least two

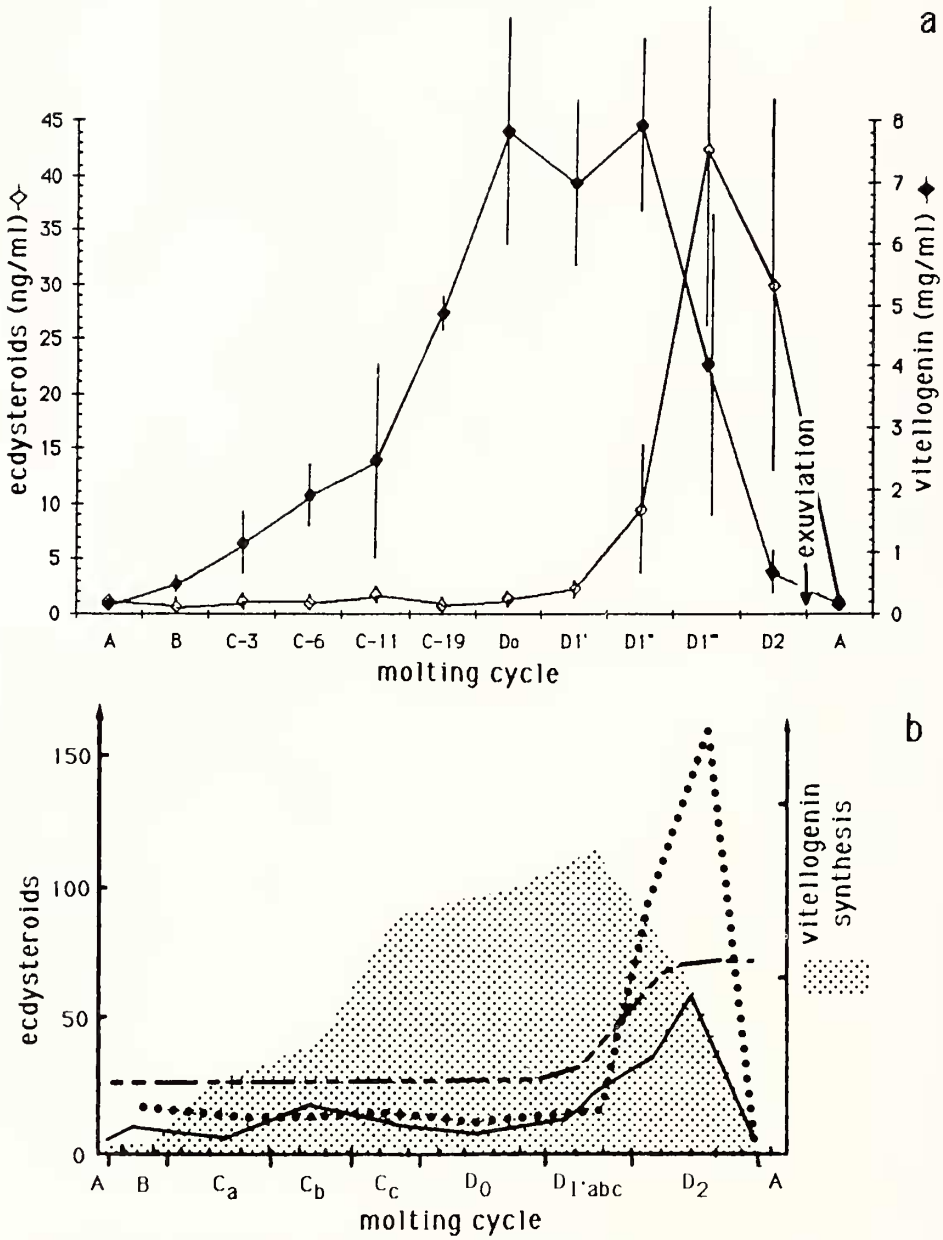

Fig. 7. (a) Evolution of the titres of circulating vitellogenin and ecdysteroids during the molting cycle in vitellogenic female prawns, *Macrobrachium rosenbergii*, of homogeneous size.
The titres of vitellogenin were determined by indirect ELISA and ecdysteroids by RIA (Derelle and Meusy, unpublished data).
Bars: standard error of the mean.
(b) Evolution of ecdysteroid titres and vitellogenin synthesis rate during the molting cycle of the female amphipod, *Orchestia gammarell* (data from [196]).
⁘⁘ : vitellogenin synthesis (see Fig. 2.a).
····· : haemolymph ecdysteroids (pg eq. 20-OH ecdysone/μl haemolymph).
– – – : ovarian ecdysteroids (pg eq. 20-OH ecdysone/mg ovary).
—— : whole animal ecdysteroids (pg eq. 20-OH ecdysone/mg fresh weight).

folds. In the same species [219], haemolymph was found to contain 10 to 50 ng/ml of methylfarnesoate and 0.003 to 0.030 ng/ml of JH-III. The highest rate of methylfanesoate in females was observed near the end of the ovarian cycle. The authors postulated a role of juvenoids in vitellogenesis, most likely mediated by the stimulation of vitellogenin synthesis.

It is noteworthy that the preceding studies have been carried out on *Libinia emarginata*, a crab exhibiting a *puberty molt* which is the last molt in its life [148]. Except the species belonging to the Oxyrhyncha's section, this feature is seldom observed in Crustacea. The reproductive physiology of such species seems more closely related to that of insects than to the majority of crustaceans. This conception seems supported by the very low level of methylfarnesoate in the haemolymph of the lobster *Homarus americanus*, a decapod which has also no puberty molt. This level is only of 1.3 ng/ml in *H. americanus* while it is of 55 ng/ml in *L. emarginata* [218]. Such a result was confirmed by the *in vitro* incubation experiments of the mandibular organs from several Brachyura and Macrura crustaceans.

The mandibular organ was also found to contain estradiol-17β and progesterone [220] (cf. Section II, B, 3).

e) Ovary-stimulating factor from males

In the freshwater shrimp, *Paratya compressa*, vitellogenesis is delayed when females are reared in the absence of males [221]. An extract of the testis or the vas deferens is able to serve as substitute for males. According to the authors, the organs of mature male shrimps, particularly the testis or the vas deferens, would secrete an ovary-stimulating pheromone which accelerates ovarian development. The presence of males has a similar effect in the isopod, *Armadillidium vulgare*; moreover, the insemination lengthens the period of ovarian activity in this species [222].

3. *Effect of other substances*

Below are gathered several experiments with various substances from male Crustacea, as well as from insects and mammals. The androgenic hormone has been proved to be non-existent in females and the occurrence of other substances acting on vitellogenesis is unknown or is a matter of discussion.

a) Androgenic hormone

As it has been demonstrated by Charniaux-Cotton (review in [175]), the androgenic gland develops only in males and controls the differentiation of the male sex. Therefore, the androgenic hormone cannot be considered as a *normal* factor controlling vitellogenesis. When the androgenic gland is implanted into females, the vitellogenin disappears from the haemolymph [223, 224], vitellogenesis stops and, in some species as *O. gammarella*, the ovary is transformed into a testis [123, 175]. More precisely, Junéra specified that synthesis in female *O. gammarella* ceased at the post-operative intermolt, or during the next following intermolt (personal communication). It is not clear whether the androgenic hormone inhibits vitellogenin synthesis directly or indirectly.

b) Vertebrate hormones

The idea that mammalian sexual hormones might be present and effective in Crustacea has led to some studies, especially on females. Bomirski and Klek-Kawinska [225] reported a positive effect of human chorionic hormone (HCG) on the ovary of the shrimp, *Crangon crangon*. After injection, they found this glycoprotein effective on vitellogenesis as well as on oogonia transformation into oocytes. The stimulation of vitellogenesis was confirmed by injection of HCG in the marine isopod, *Idotea balthica basteri*, and an increasing rate of vitellogenin synthesis and liberation was also observed [226]. This effect seems specific for vitellogenin since the rate of total protein synthesis was not modified.

A stimulatory effect of progesterone on the development of the oocytes of the penaeid prawn, *Parapenaeopsis hardwickii*, seemingly on vitellogenesis, was also reported [227].

An estrogenic activity was recognized for long time in tissues of the lobster, *Homarus americanus*, especially in eggs [228–230]. In the same species, Lisk identified the estrogenic activity to be estradiol-17β and did not detect any estrone [346]. The presence of estrogen-like compound was also reported in the ovary of the shrimp, *Parapenaeus fissurus* [231]. Ollevier *et al.* [232], using mass spectrophotometry, identified five nonecdysteroid

steroids in the haemolymph of male and female *Astacus leptodactylus*: pregnenolone, 17β-hydroxypregnenolone, testosterone, cholesterol and 6β-hydroxyprogesterone. Recently, Couch *et al.* [220] found progesterone-like and estradiol-like immunoreactivity in the mandibular organ, green gland, hepatopancreas, ovary and serum of *H. americanus*. They showed that these steroids change in concentration in relation to the development of the ovary and suggested that estradiol-17β, or one of its metabolites, could promote vitellogenesis in Crustacea as it acts in egg laying vertebrates. Further studies would be necessary to put forward well-stated hypotheses about the role of vertebrate-like hormones in Crustacea

c) "Queen-substance" of honeybees

It is known that the "queen-substance" of honeybees inhibits the development of the worker's ovaries and the production of further queens, probably through the inhibition of corpora allata growth (review in [233]). According to Carlisle and Butler [234], this substance shows an inhibitory effect on the development of the prawn's ovaries and, in a reciprocal way, the extract of sinus glands from *Palaemon serratus* inhibits the ovary development in worker honeybees. This result, which has not yet been confirmed, might indicate some chemical similarities between the "queen-substance" and VIH.

4. *Environmental factors and vitellogenesis*

Among environmental factors, photoperiodism and temperature were the most investigated (cf. [235], for review).

a) Light and temperature

Light seems the most prominent factor for controlling reproduction, but temperature seems to have also an effect, perhaps indirect (Table 1). As we could expect, light has various effects depending on the natural environment of the species, the history of the animal (i.e., the environmental conditions before the experiment), the stage of the ovary at the onset of the experiment, etc. For instance, vitellogenesis is induced by long day photoperiods in the southern amphipod, *Gammarus lawrencianus*, which produces sequential broods during spring and summer; in contrast, short day photoperiods promote vitellogenesis in another species, *Gammarus setosus*, which is found in high latitude and produces a single brood at the very beginning of the year [240]. Though it is undoubtful that environmental factors act on reproduction *via* VIH, perhaps together with some other neurohormones, the relationship between the receptors for environmental factors and the neurosecretory system remains to be studied.

b) Other factors

Extensive studies were carried out on aquacul-

TABLE 1. Effect of light and temperature on vitellogenesis and reproduction in malacostracans

Species	Author(s)	Factor(s)	Results
Amphipoda			
Pontoporeia affinis	Segerstrale (1970) [236]	Light	Constant light → inhibition of gonad development. Decrease in illumination → "maturation" process.
Gammarus setosus	Steel *et al.* (1977) [237]	Light	Short days → acceleration of reproductive cycle. But the cycle is not completely controlled by photoperiod and cannot be stopped.
Hyalella azteca	de March (1977) [238]	Light and temperature	Long photophase → reproduction (main factor). Temperature → effect on the rate of all reproductive changes.
Gammarus lawrencianus	Steele (1981) [239]	Light	Short days → resting stage.
G. lawrencianus and *setosus*	Steele and Steele (1986) [240]	Light	Short day photoperiods → vitellogenesis in *G. setosus* → opposite effect in *G. lawrencianus*.
Gammarus lacustris	de March (1982) [241]	Light	Decreased photophase → reproduction.

TABLE 1. (Continued)

Species	Author(s)	Factor(s)	Results
Isopoda			
Oniscus asellus	McQueen and Steel (1980), Steel (1980) [242, 243]	Light and temperature	Long days → induction of reproduction (temp. affects molting and has no direct effect on reproduction). Seasonal periodicity in the responsiveness of females.
Armadillidium vulgare	Juchault *et al.* (1982) [244] Jassem *et al.* (1982) [377]	Light	Increased photophase over 12–14 h → reproduction.
Decapoda (Penaeidea)			
Penaeus japonicus	Laubier-Bonichon (1975, 1978) [245, 246]	Light and temperature	Long photophase (L = 13.5–16 h) and high temp. (24–26°C) → stimulation of breeding.
Decapoda Astacidea			
Cambarus	Stephens (1952) [247]	Light	Dailylight periods (any duration) → periodic resorption of yolk. Continuous darkness → oocyte "maturation".
Orconectes virilis	Aiken (1969) [248]	Light and temperature	4–5 months of low temperature and constant darkness are necessary for complete "maturation" of the oocytes in lab. experiments.
Procambarus clarkii	Suko (1958) [249]	Light	Total darkness → effect depending on the initial stage of the ovary.
Cambarellus shufeldti	Lowe (1961) [250]	Light and temperature	Increased photophase and temperature → acceleration of oocyte "maturation" and yolk resorption.
Orconectes limosus	Kracht (1972) [251]	Light and temperature	Artificial season able to promote anticipation of breeding, hatching and molting.
Orconectes nais	Armitage *et al.* (1973), Rice and Armitage (1974) [145, 252]	Light	Long-day photoperiod → inhibition of ovarian growth. Short-day photoperiod → acceleration of ovarian growth. Gonadal growth and molting are negatively related.
Homarus americanus	Nelson (1986) (+earlier references from other authors) [253]	Light and temperature	In some populations: 2–3 months of short-days are necessary to condition the ovary for vitellogenesis following long-day onset. No requirement for European species (*H. gammarus*).
Decapoda Brachyura			
Menippe mercenaria	Cheung (1969) [130]	Temperature	Higher spawning frequency during hot months (even if the days are not the longest).
Pachygrapsus marmoratus	Pradeille-Rouquette (1976) [254]	Light	Long photophase → vitellogenesis only if the animals have been subjected to a short photophase before.
Scylla serrata	Nagabhushanam and Farooqui (1981) [255]	Light	Long-day photoperiod (14L: 10D or more) favours vitellogenesis.

ture species to improve the production of farming: for instance, about the composition of feeding pellets with the aim of promoting growth and/or vitellogenesis, about the density of population, nature and color of the substratum, and salinity. Such applied investigations are generally reported in aquaculture journals.

Some other factors have been the matter of studies. For instance, noise, at the level of 30 dB, has a negative effect on female reproduction of the

sand shrimp *Crangon crangon* [256]. Lunar phases seem also to have an influence on reproduction: ovaries of the crabs, *Uca tangeri* and *U. terpsichores*, are the most highly developed around full moon [257–259].

5. *Parasitism and vitellogenesis*

In female decapods, parasitic infestation due to rhizocephalans leads to an atrophy of the ovaries chiefly due to an abortive vitellogenesis. Although such an effect was described in several crabs (*Macropodia rostrata, Carcinus mediterraneus, Pachygrapsus marmoratus* and *C. maenas*) [37, 260–262], the causes and the modalities of the gametogenesis impairement still remain not well known. A penetration of the rhizocephalan's root system across the ovarian wall and its close contact with the oocytes have been reported in *M. rostrata* parasitized by *Sacculina fraissei* as well as *C. maenas* and *C. mediterraneus* parasitized by *S. carcini* [32, 260].

In both *Carcinus*, the growth of oocytes does not progress beyond a diameter of 120 μm that corresponds to the end of previtellogenesis. Oocytes never develop further and do not reach an average size of 350 μm that is normally observed in vitellogenic ovaries of non-infested crabs. Preliminary ultrastructural studies indicate that this blocking is partly due to abnormality in the organization of the vitellogenic follicle: follicle cells remain at a certain distance from the oocytes, instead of surrounding them tightly as in healthy females. At their terminal evolution, oocytes agglomerate and then unite before being resorbed by hemocytes and some follicle cells, later on. This lysis phenomenon is quite comparable to the one that occurs following AG implantation into destalked females or topical application and ingestion of a juvenile hormone mimic [206, 263]. In both circumstances, there is no egg laying. Hormonal imbalances related to the presence of the parasite appear responsible for this inhibition [264]. A biochemical and immunochemical investigation of vitellin proteins from the ovary and haemolymph was recently performed in healthy and parasitized *C. maenas* [265]. This study shows that the ovarian development arrest would be due to an inhibition of the control of the vitellin synthesis and vitellogenin uptake by the gonad. The vitellin proteins of *Sacculina* do not display any electrophoretic or immunochemical similarity to those from the host.

III. OOCYTE MATURATION

In malacostracans, the mechanism of oocyte maturation or meiotic maturation, i.e., meiotic resumption of the arrested-prophase I oocytes, occurs in the ovary and begins before fertilization. Very few histological descriptions have been devoted to this phenomenon. Beside those reported in some amphipods [266, 267], two recent cytological studies were carried out in *Orchestia gammarella*, and then in the prawn *Palaemon serratus* [268, 269]. They report the events which lead to the release of the first meiotic block and are closely linked in time with the preparation of the molting phenomena (Fig. 8).

The chronology of the cytological aspects has been recently established in *P. serratus* [270]. Initially arrested at prophase I, the oocytes resume meiosis when approaching stage $D_{1^{+}}$ of the molt cycle (4 to 5 days before molting). This premolt period is characterized by the following steps: nuclear envelope folding, nucleolar regression and dissociation, condensation of the chromosomes and beginning of the breakdown of the nuclear envelope. The germinal vesicle breakdown takes place at the $D_{1^{+}}$-early D_2 stage, when the germinal vesicle still occupies a central position in the oocyte. Migration of the broken germinal vesicle that holds chromosomes occurs at the end of the D_2 stage, i.e., approximately 4 hr before exuviation. The divalent chromosomes that are not yet organized in a metaphase plate become visible at the oocyte surface, only 1–2 hr before the exuviation. They lay in a nucleoplasmic region devoid of nuclear envelope. The first meiotic spindle can be seen at the time of exuviation. The oocytes remain blocked at this stage of metaphase I until spawning.

To determine the exact stimulus that governs meiosis resumption, experimental studies have been conducted in *O. gammarella* and *P. serratus* [268, 269]. In *O. gammarella*, if exuviation is advanced by injection of 20 OH-ecdysone or de-

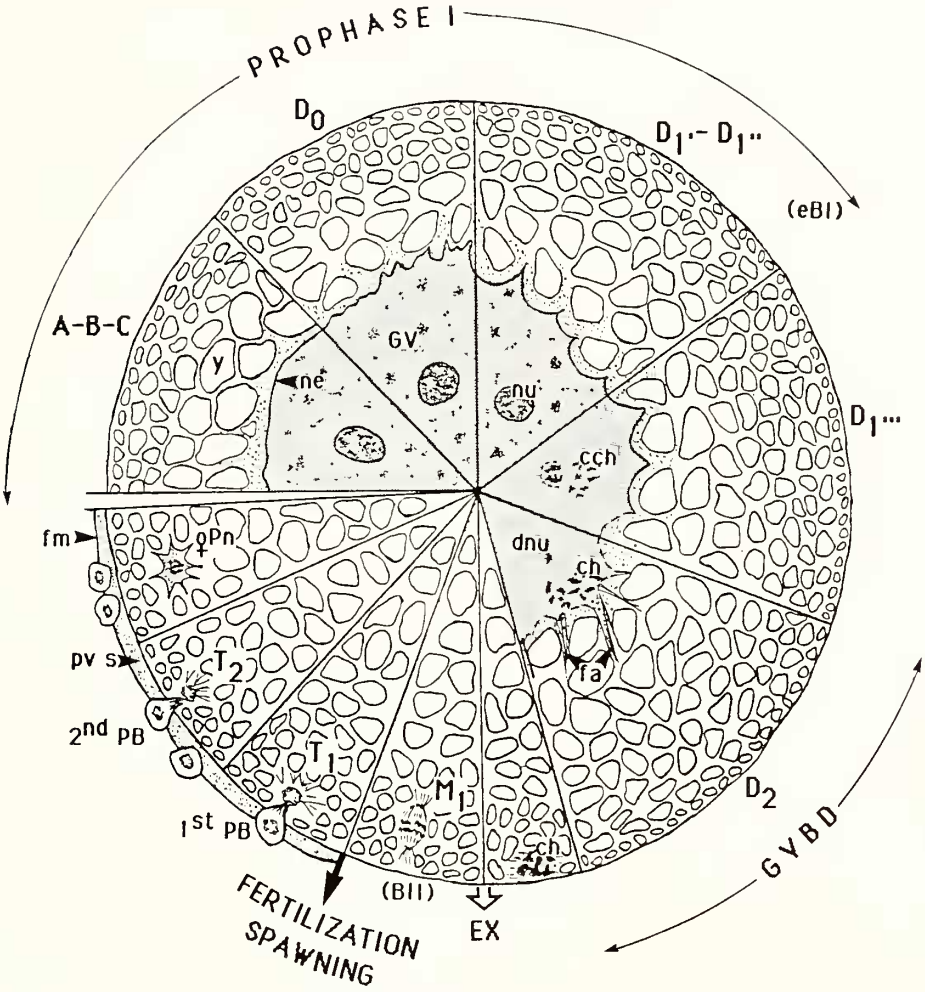

FIG. 8. Diagram showing the evolution of the nuclear apparatus during maturation and activation processes in the prawn *Palaemon serratus* (redrawn from [270]).
A, B, C, D_0, D_1', D_1'', D_1''', D_2: stages of the molt cycle; cch: condensed chromosomes (ch); dnu: dissociation of nucleolus; Ex: exuviation or maturation molt; eBI: end of the first blocking stage in prophase 1; BII: second blocking in metaphase 1 (M1); fa: filamentous apparatus; fm: fertilization membrane; GV: germinal vesicle; GVBD: germinal vesicle breakdown; ne: nuclear envelope; nu: nucleolus; 1st PB, 2nd PB: first, second polar bodies; pvs: perivitelline space; T1, T2: telophase 1 and 2; OPn: female pronucleus; y: yolk body.

layed by cauterization of the median zone of the protocerebrum, the two phenomena remain simultaneous only if the oocytes have reached a certain size (about 500 μm of diameter). Furthermore, if exuviation is blocked by Y-ectomy, no maturation occurs. In *P. serratus* meiotic reinitiation of prophase I blocked – oocytes is triggered if immature oocytes are incubated in presence of either 20 OH-ecdysone (10^{-6}M), or ponasterone A, or ionophore A 23187 (5 μM in a normal or Ca^{2+} free seawater milieu). These results suggest that steroids are involved in meiotic maturation. To our knowledge the only comparable data in the other arthropod concern the insect *Locusta migratoria* [271]. Moreover, in the prawn, the treatment with ionophore indicates that steroid inducers may act via intracellular calcium. It is tempting to correlate Clédon's results with those that mention a high

concentration of ecdysteroids in the ovaries of the shore crab *Carcinus maenas* at the end of vitellogenesis (10^{-6} M compared to 10^{-8} M in the haemolymph), as well as in the eggs immediately after egg laying [204, 272]. If there exists a relationship between ecdysteroids and the resumption of meiosis, do steroids primarily at the level of oocyte membrance induce a cascade of events similar to those known in amphibian oocyte [273], or only after their entrance into the ooplasm where they accumulate?

IV. OVULATION

The process by which oocytes are expelled from the ovarian environment (ovarian spawning) has been rarely studied in crustaceans and must be distinguished as a separate process from oviposition that is the release of oocytes or eggs in the external milieu.

The only available description of ovulation has been carried out by Fauvel [274] in the prawn *Macrobrachium rosenbergii*. In this species, it occurs after ecdysis when the follicle epithelium retracts at the periphery of the ovary, i.e., when

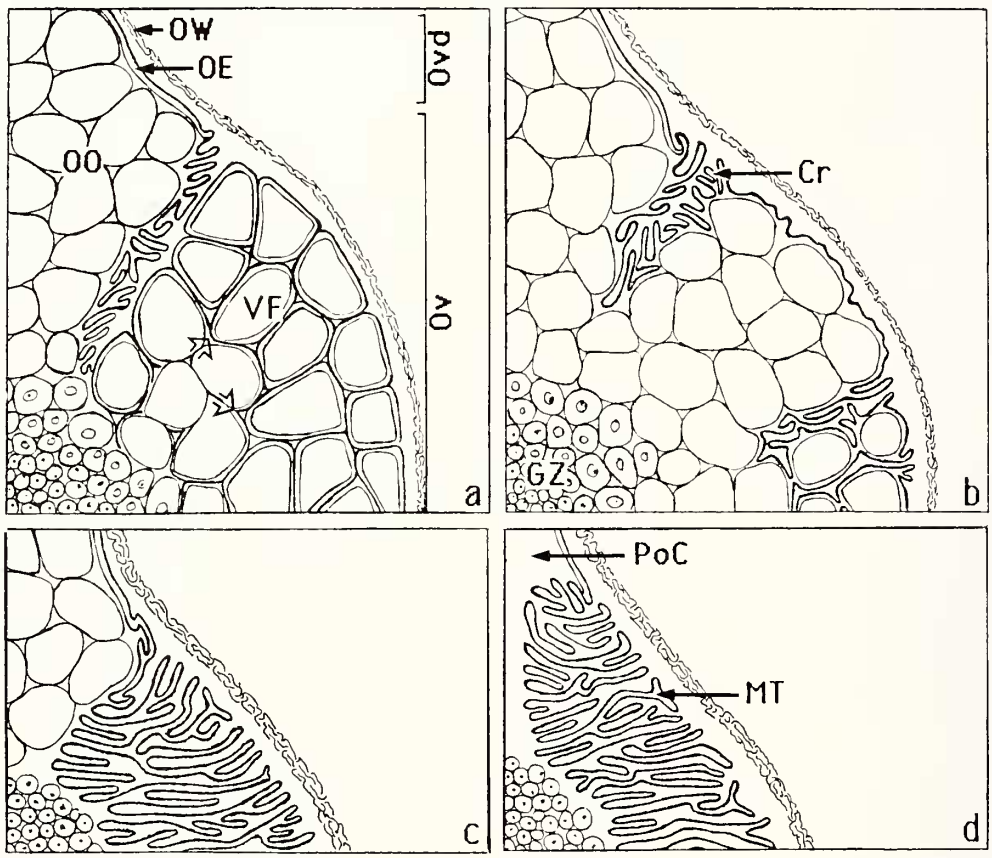

FIG. 9. Phases of ovulation in the prawn, *Macrobrachium rosenbergii* (adapted from [274]).

a. At the beginning of ovulation the follicle epithelium retracts from the vitellogenic oocytes (arrow) located near the oviduct (Ovd).

b. Course of ovulation. Retracted mesodermal tissue forms crests (Cr) between the ovulated oocytes (OO) at the periphery of the ovary (Ov).

c. and d. End of ovulation. The follicle tissue occupies the empty space left by the spawned oocytes.

MT: mesodermal (follicle) tissue; OE: oviducal epithelium; OW: ovarian wall; PoC: perioviducal cavity; VF: vitellogenic follicle; GZ: germinative zone.

the follicle envelope separates from the oocyte (Fig. 9). The retraction begins in an ovarian zone close to the oviduct. Then, crests of retracted mesodermal tissue are formed between the ovulated oocytes. At last, the follicle tissue occupies the empty space left by the spawned oocytes. This tissue, which always develops in continuity with the epithelium of the oviduct and remains in the peripheral region of the gonad, is used again for a new folliculogenesis. Although evidence of a direct hormonal intervention in ovulation has not yet been reported, we must mention that Matsumoto [275] described an increased neurosecretory cell activity associated with ovulation in the crabs *Potamon, Sesarma, Neptunus* and *Chionocetes*. It is not sure that ovulation is used by the author with the above meaning.

V. OOCYTE ACTIVATION

Oocyte activation allows the completion of meiosis. It is characterized by the release of the second meiotic block which follows exuviation. It leads to both the extrusion of the polar bodies and the elaboration of the fertilization membrane. At last, the female pronucleus is formed, ready to fuse with the male pronucleus to make a zygote.

Among the sequence of morphological events that characterize fertilization and lead to the spermatozoon-oocyte association, we shall limit our interest to two aspects: 1) the fertilization potential, 2) the cortical reaction, i.e., the response of the oocyte plasma membrane to the spermatozoon penetration. Therefore, we do not describe the initial events of the gamete contacts and particularly the acrosome reaction that fits better in a review on male reproduction. Indeed, a number of well-documented papers dealing with this topic concern the decapods which show the particularity to have non-motile spermatozoa (cf. e.g., [276–281]).

A. Meiosis reinitiation of metaphase I - arrested oocytes

It is now well-known that oocytes of amphipods and several decapods are at the first meiotic metaphase at the time of spawning and meiosis resumes soon thereafter [266–269, 281–289]. Anaphase stage takes place in the spawned eggs. For a long time it has been uncertain whether spawning or fertilization triggers meiosis to complete. In order to elucidate this question, different experiments were undertaken on *Palaemon serratus*. It thus appears that the release of the second meiotic block can be obtained *in vitro*, in presence of an excess of extracellular calcium (10 to 30 mM), or KCl (60 mM), or ionophore A 23187 (5 μM) [269]. As for the resumption of the first meiotic block, the stimulation by A 23187 requires the presence of Ca^{2+}. In addition, experimental fertilization performed *in vitro* indicates that in *P. serratus*, fertilization is responsible for the second meiotic resumption [269, 270]. However, other works carried out on the same prawn have shown that meiosis resumes when the egg comes into contact with seawater, independently of fertilization [288]. Investigations concerning a possible ionic control of activation have led to the conclusion that the presence of external Mg^{2+}, but not the external Ca^{2+}, is required for resumption of metaphase I in *P. serratus* oocytes. It is the change from the low Mg^{2+} environment of the ovary (10 mM) to the high Mg^{2+} of seawater ($\geq$15 mM) that stimulates meiosis to resume. Therefore, activation occurs at spawning and does not require fertilization [289]. No indication yet concerns a possible role of extracellular Mg^{2+} for the spermatozoon-oocyte fusion.

An electrophysiological study completes the above results. It states that an increased oocyte membrane permeability to K^+ occurs at spawning in *P. serratus*. It is not dependent on fertilization but depends on the increase in external Mg^{2+} concentration at spawning. In other words, at spawning, the hyperpolarization of the oocyte membrane to K^+ only occurs in presence of a sufficient external Mg^{2+} concentration [289].

B. Fertilization potential

In contrast to various animal groups in which the electrical characteristics of oocytes at different steps of their development, including fertilization, have been described (cf. reviews [290, 291]), the electrical response to fertilization was evidenced quite recently in malacostracans. The investigations concern the crabs *Carcinus maenas* and *Maia*

squinado, and the lobster *Homarus gammarus* [287, 290, 291]. They show that the fertilization potential consists of a sustained hyperpolarization of the egg membrane (from −32 to −62 mV in the crabs). In these decapods, *in vitro* insemination revealed a sperm-triggered increase in the ionic permeability of the egg membrane which becomes selective for K^+, whereas before insemination it was predominantly selective for Cl^-. This instantaneous shift that constitutes the fertilization potential seems to be promoted by a rise in cytoplasmic-free Ca^{2+} that might mediate the hyperpolarization. It occurs concurrently with the second meiotic reinitiation in the metaphase I-arrested oocytes. It must be pointed out that under natural conditions, the early events in crab fertilization take place internally in the female genital duct and sometimes in the lumen of the ovary [128, 280, 282, 292, 293], whereas the lobster oocytes are fertilized in the external environment [294]. It thus appears that the electrical response of the oocyte to fertilization may reflect a general property of reptantian Decapoda. As already pointed out (cf. Section V, A) in the prawn *Palaemon serratus* in which fertilization is external (the extruded oocytes pass over the spermatophore previously deposited by the male at mating), a similar increase in K^+ conductance of the oocyte membrane takes place at spawning. This increase is not dependent on fertilization, but depends on an increase in external Mg^{2+} concentration at spawning [289]. Until now, the egg's electrical response to fertilization remains to be explored in *Palaemon.*

C. Cortical reaction

The cortical reaction can be defined as one of the anatomical responses (besides the formation of the fertilization cone and the elaboration of the first polar body) of the oocyte developing an hyperpolarization response after insemination. However, this phenomenon may be also initiated after exposure to sea water.

The morphological events that occur in the cortex of eggs, i.e., the exocytosis of cortical granules into the perivitelline space and the transformation of the plasma membrane were investigated by means of scanning and transmission electron microscopy in the penaeid shrimps *Penaeus aztecus* and *P. setiferus,* and the shore crab *Carcinus maenas* [295–297]. A brief description of the cortical granules has been also reported in the amphipod *Orchestia gammarella* [4, 91]. We shall examine the cortical reaction process respectively in these three models, although it must be known that the elaboration of the fertilization envelope was described in detail in cirriped eggs [298].

During the cortical reaction, early fertilized *C. maenas* eggs maintained under *in vitro* conditions appear to release successively: 1) a fine granular material that accumulates in about 15 min on the inner face of the vitelline envelope [296] and, 2) a massive amount of ring-shaped elements which coalesce to give rise to a new thick coating underlying the vitelline envelope and represents most of the fertilization envelope. This phenomenon lasts about 7–8 hr. The ring-shaped elements come from egg cortical vesicles. It was established by Goudeau [297] that these elements and their enclosing vesicles originate in the endoplasmic reticulum from which they are released by direct endocytosis. The author considers that the ring-shaped elements are precursors common to the cortical exudate and to the endogenous yolk (cf. Section II, A).

The cortical reaction in the eggs of penaeids is unique with respect to: 1) the size of the cortical specializations (rods that are around 40 μm length for an egg diameter of about 270 μm), 2) the rapid expulsion and dissipation of these elements in response to sea water, 3) the decrease in the egg volume after the reaction. The rods are always located perpendicular to the oolemma and composed of numerous tightly packed fibrillar structures. Each cortical rod lies within a partially membrane bound crypt and is separated from the external environment by a thin coat that completely surrounds the egg. As the rods are expelled in the sea water, a corona forms around the oocyte and then quickly dissipates. Simultaneously an extensive membrane vesiculation associated with cortical rod crypts become apparent around the entire egg surface and later forms a homogenous jelly. Mg^{2+} ions and a protease dependence of this jelly release have been demonstrated in *Penaeus*

and in another penaeid, *Sicyonia* [279, 281, 299].

In *O. gammarella*, cortical granules have been observed towards the end of vitellogenesis when the oocytes are no longer attached to the follicle tissue due to the retraction of the macro- and microvilli. At this period, the vitelline envelope becomes thick. The cortical granules are oval-shaped and measure 0.2–0.3 μm of mean diameter. They become visible when the microcanals and pinocytotic vesicles disappear. They display lamellae alternatively lucent and electron dense and are bound by an outer membrane. Glycoproteins have been detected. After fertilization, the cortical reaction consists of two steps. The first shows a fusion of the cortical granule membrane with the egg plasmic membrane, leading to the release of granule contents into the perivitelline space. During the second step, the vitelline envelope is elevated off the surface of the oocyte and acquires on its inner face an opacity that rapidly extends to the outer face. This opacity is concomitant with important modifications of the vitelline envelope that becomes the fertilization envelope. The origin of the cortical granules and the duration of the cortical reaction remain to be studied in this peracarid.

VI. OVIPOSITION

Generally, oviposition takes place when the environmental conditions are favorable for embryonic development. Thus, according to the geographical distribution of the species, oviposition is spread over a season or restricted to some months (cf. for review [235, 300]). In peracarids and some natantians, this phenomenon is usually preceded by a molt, whereas it is confined to intermolt in many brachyurans.

A few results concern the existence of a control of oviposition by an eyestalk factor. They have been obtained from diverse eyestalk-ablated decapods:

—In juvenile *Carcinus maenas* the operation leads to a precocious vitellogenesis and spawning may follow but, since the puberal form of the external sex characteristics is not completed, the eggs do not remain attached to the pleopods [301]. According to the author, a factor linked to the presence of eyestalks would be involved in the development of the female external sex characteristics.

—Postmolt crabs, *Menippe mercenaria*, spawn precociously without undergoing accelerated ovarian development [130]. This may be an argument in favor of the fact that spawning and ovarian development would be controlled by different eyestalk hormones.

—However, in juvenile prawns *Penaeus japonicus*, oviposition never follows the accelerated vitellogenesis because the oocytes degenerate (Laubier and Bizot-Espiard, personal communication). Similarly, in the crabs *Rhithropanopeus harrisii* and *Paratelphusa hydrodromous* eyestalks would be necessary to the process of oviposition at time of the reproductive period [302, 303]. Moreover, the oviposition-inducing hormone would be released several days before spawning.

Environmental factors such as water temperature and photoperiod, probably channeled through the neuroendocrine system, seem also to affect oviposition, as has been shown in the crayfish *Orconectes virilis* [248, 304] and the crab *Pachygrapsus marmoratus* [285]. Synchronization of oviposition with specific tidal phases has been also reported in the stomatopods *Gonodactylus zacae* and *G. falcatus*. [305]. Spawning postures have been described for the spider crab *Chionocetes opilio* and the spiny lobster *Panulirus homarus* [306, 307].

In contrast to insects in which oviposition is a fully-studied event beginning shortly after mating (cf. review [308]), more thorough investigation is needed in crustaceans because this process occurs either after or before mating, depending on the considered species (cf. Section V, B).

VII. SEX CHARACTERISTICS ASSOCIATED TO SPERM STORAGE, MATING AND EGG INCUBATION

Among the female characteristics related to sperm storage, mating and egg incubation, one can distinguish specialized regions of the genital duct of species in which fertilization occurs internally and structural modifications of some body segments, as well as of different appendages.

A. Genital duct

The most original feature of the genital duct of some malacostracans is the spermatheca (seminal receptacle), a specialized area that receives the spermatophores in which spermatozoa are stored. The presence of spermatheca is essentially known in brachyurans. Study of the genital apparatus morphogenesis carried out in the crab *Rhithropanopeus harrisii* [11] reveals that, beginning at the fourth postlarval stage, one can determine in the female genital duct three distinct regions from the gonad to the sexual orifice, or vulva: an oviduct, a spermatheca and, distally, a vagina. This is in agreement with Hartnoll's description [309]. The oviducts shorten when the spermatheca develop. In puberal crabs, the cuticle lines the walls of the spermatheca. A scanning electron microscopy examination of the luminal wall of the genital duct of *Carcinus maenas* reveals that, at the level of the spermatheca, the epithelium and the cuticular covering form numerous parallel folds and differentiate two lateral pouches filled with stored spermatozoa [293]. Such an anatomical pattern explains sperm retention after mating for several successive reproductive periods separated by molts [310]. In addition, Anilkumar and Adiyodi [311] reported a cyclic synthetic activity of the spermatheca epithelial cells of the crab *Paratelphusa hydrodromous* in relation to the reproductive cycle.

The oviducal epithelium of the shore crab differentiates during the reproductive premolt period two distinct secretory zones that are supposed to be involved in the release of a sexual pheromone attracting the male for copulation. Another interpretation of Anghelou-Spiliotis and Goudeau [293] is that the secretions could have also a lytic function on the spermatophore walls. At last, when the oocyte is ready to be spawned, these substances could be involved in the modification of the chemical composition of the vitelline envelope.

B. External sex characteristics

The external sex characteristics only present in females and involved in specific functions are either permanent or temporary. The permanent characteristics generally develop in the juvenile females. They are: 1) the shape of the last thoracic sternite which bears an external seminal receptaculum in caridean shrimps or a thelycum in penaeids, 2) the oostegites in some peracarids. The temporary characteristics include: 1) the sexual setae used for pairing, 2) the oostegites in some isopods, 3) the ovigerous setae (oosetae) of amphipods and decapods, 4) the brood chamber of Caridae. These last three characteristics are associated with the incubation of embryos.

1. *Differentiation*

As an example of permanent female characteristics we have chosen to describe the development of the oostegites that has been well-studied in the amphipod *O. gammarella* [123]. Oostegites appear as small outgrowths on the internal face of the coxae of the second gnathopod and pereopods 3, 4, and 5. At that time, the ovaries contain follicles with previtellogenic oocytes. The oostegites develop further at each molt and form the brood pouch or marsupium in the puberal female. During development of the oostegites in the young females, trichogenic matrices are set up. They form short setae (0.02 mm in length). Almost all amphipods possess four pairs of oostegites; however, this number can vary, as in Caprellidea, where only two pairs of oostegites are born by segments 3 and 4 [312]. In *O. gammarella,* during the reproductive season, a vitellogenesis occurs during each molt cycle, and spawning after each ecdysis. During stage D of the molt cycle, the trichogenic matrices form long setae (0.8 mm in length) which appear at ecdysis. These setae border the oostegites and ensure a good closing of the brood chamber. They are temporary sex characteristics associated with the incubation of embryos. They are replaced by short setae during the intermolt cycles without vitellogenesis [123].

Females of isopods also possess oostegites. These sexual appendages are permanent characteristics in *Ligia oceanica, Helleria brevicornis* and the aquatic species *Asellus aquaticus, Sphaeroma serratum* and *Idotea balthica* [125, 152, 313–315]. They acquire their functional form only at molts followed by egg laying and again take their non-functional form at the period of genital rest.

Their functional form can be considered as a temporary characteristic related to egg incubation. However this is not the case in the aquatic isopod, *Idotea balthica,* in which the functional form persists throughout the life span of the female. In Oniscidea, except Ligiidae and Tylidae, the presence of oostegites constitutes a temporary characteristic which only appears at time of the molts followed by egg laying and disappears at time of genital rest. In *I. balthica,* another temporary characteristic concerns the sexual setae born on the internal surface of the second pereopods which disappear at the molt preceding the first egg laying [125, 316].

The morphological modifications leading to the formation of the brood chamber in Caridea have been particularly studied in some Palaemonidae [317], *Atyaephyra desmaresti* [318] and *Macrobrachium rosenbergii* [23]. However, no correlation with the developing ovaries has been noted. The brood chamber is not permanent in some Palaemonidae. It disappears during genital rest. Indeed, coxopodites and sternites take again the juvenile form. No study concerns the trichogenic matrices. The brood chamber is formed by broadening of the sternites and lengthening of the coxopodites of the first three somites of the pleon. Basipodites enlarge and display a groove-like shape, with the concavity turned to the rear. An effective closing of the brood chamber is ensured by long plumose setae arranged in two rows on each basipodite. The eggs are attached to the ovigerous setae (oosetae) which are located on the internal edge of the basipodites. The newly laid eggs are guided to the seminal receptaculum by means of long setae both on the coxa of the pereopods 3, 4 and 5, and around the gonopores.

In female crabs, four pairs of unsegmented and hairless biramous pleopods develop from the third crab stage, on the second to the fifth abdominal segments. Segmentation of the endopodites, and exopodites generally precedes by one stage the appearance of tufts of hairs on the endopodites and of a setiferous fringe on the endopodites [11, 319]. In the crab *Pachygrapsus marmoratus,* as in caridean shrimps, oosetae develop on the pleopods and along the edge of the abdominal sternites at the molts that are followed by egg laying; the oosetae disappear when the ovary is at rest [320]. These temporary characteristics appear for the first time during the molt preceding the first egg laying. In some species, such as *Carcinus maenas,* the abdomen acquires the female form (enlarging, curving inwards, and hairs on pleopods) at the puberty molt that occurs one or several molts before the first egg laying [301, 321]. The external characteristics acquire their definitive shape only at the final puberty molt in brachyurans that undergo a limited number of molts as the Majidae [322, 323], the Leucosiidae, and the Portunidae of the genus *Callinectes* [324, 325]. In the Majidae *Acanthonyx lunulatus* and *Libinia,* the first egg laying occurs immediately or sometime after the puberty molt [326, 327]. Indeed, in these two species, the first vitellogenesis begins respectively during the course of the last intermolt cycle and after puberty.

The mechanism that allows a newly laid egg to be attached to ovigerous setae has been studied in the crab *Carcinus maenas* [128, 328]. It involves the formation of a funiculus that originates from the two superimposed vitelline envelopes [92, 286].

Examination of the structure of the funiculus and of the morphological features of its binding to maternal egg-carrying setae revealed that the tip of the funiculus is coiled around the setae without adjunction of any additional attachment substance. Four concentric envelopes which are successively secreted by the ectodermal embryonic cells underneath the fertilization envelope have been detected during the embryo development. It is noteworthy that ponasterone A, an ecdysteroid present in high concentration, would be involved in the deposition of the embryonic envelopes [328].

In some species, special secretions of tegumental glands of the ventral abdomen seem to be used for attachment of eggs. For example, Mason [329] indicates that the oviposition posture leads to the formation of a water-filled cavity into which the eggs of the crayfish, *Pacifastacus leniusculus trowbridgii,* pass brushing across the glandular areas. Moreover, it has been noted in another crayfish, *Austropotamobius pallipes,* that the activity of these glands is possibly linked to egg growth [330].

At last, these glands would have also a role in dissolution of the spermatophore wall and transport of spermatozoa [329].

An ultrastructural analysis of the pleopod tegumental gland in the lobster, *Homarus americanus*, was recently carried out [331]. It completes a previous study in the same species by Aiken and Waddy [332]. The pleopods of both male and female lobsters contain rosette type glands. However, they are most abundant in females with well-developed ovaries. Two types of secretion seem to be produced continually. They would be involved in the hardening of the cuticle after molting and also in condensation and hardening of the outer egg coat during egg attachment to the ovigerous setae.

2. *Regulation of development*

An ovarian control of external female characteristics has been demonstrated in several peracarids. Such a control mechanism has been reported in various reviews [123, 333–336]. In decapods, attempts at surgical removal of the ovaries have not so far been successful and there is only an indirect proof of the existence of ovarian hormone(s) [337].

In *O. gammarella*, the ovaries control the permanent and temporary characteristics. The control of oostegites (permanent characteristic) has been studied by implantation of a young or fully-developed ovary into a male from which AG have been removed. In both circumstances, oostegites appear at the first or second postoperative molt. The follicle cells of previtellogenic oocytes seem to be the source of the ovarian hormone responsible for the formation of oostegites. Since this hormone is secreted throughout the life span of the female, Charniaux-Cotton and Payen [336] proposed to call it "Permanent Ovarian Hormone" (POH). The induction of oostegites by POH is irreversible: it persists in castrated females.

In some isopods, as *Idotea balthica* and *Ligia oceanica*, the oostegites differentiate in young females without the mediation of a hormone. In castrated females, the marsupium develops normally [125, 152, 316]. In addition, a marsupium develops in andrectomized males of *I. balthica* although the testes are not reversed into ovaries.

The experimental results obtained in *O. gammarella* and few isopods (*Armadillidium vulgare*, *Porcellionides pruinosus* and *Porcellio laevis*) [77, 338–340] show that the ovary secretes during vitellogenesis a hormone controlling the formation of the temporary external characteristics. Charniaux-Cotton and Payen [336] have called it "Temporary Ovarian Hormone" (TOH).

In *O. gammarella*, ovariectomy during the reproductive period is followed by replacement of ovigerous setae by juvenile setae [77]. Likewise, when a vitellogenic ovary is implanted into an andrectomized male, the induced oostegites acquire ovigerous setae. The follicle cells of the vitellogenic oocytes seem to be the source of TOH. The formation of ovigerous setae requires also the presence of molting hormone. During genital rest, when 20 OH-ecdysone acts alone, juvenile setae are formed. If the quantity of ovarian hormone does not attain a certain threshold, as after a partial ovariectomy, the elongation of the trichogenic matrices is only partial and, as a result, the length of the setae is intermediate. When molting and ovarian hormones are present, the matrices stretch out extensively and form ovigerous setae.

In *Armadillidium vulgare* and *Porcellio dilatatus*, the oostegites (temporary characteristic) never appear in ovariectomized females [338, 341, 342]. Reimplantation of a small ovarian portion induces the formation of an incomplete marsupium.

In decapods, in the absence of successful ovariectomies and implantations, the control of permanent female characteristics is not known. Temporary external characteristics appear to be controlled by vitellogenic ovaries, as in peracarids. Implantation of portions of early vitellogenic ovary into AG ablated male freshwater prawns *Macrobrachium rosenbergii* [337] results in the induction of female breeding characteristics as ovigerous and ovipositing setae and brood chamber. Indeed, these characteristics develop during vitellogenesis and disappear when the ovaries are resting. These relationships between the morphogenesis of the temporary characteristics and the course of vitellogenesis remain to be precised. However, it is worthy to note that the existence of an ovarian hormone controlling the external sexual character-

istics was suggested in the forties by some authors who studied the effects of parasitic or X-ray castration on the shrimp *Leander* (*Palaemon*) *serratus* [343]. Furthermore, at the same time, evidence of a correlation between ovarian and tegumental gland development was noted in the shrimp *Crangon crangon* and in the crayfishes *Cambarus virilis* and *C. rusticus* [304, 344].

VIII. SEX RECOGNITION AND MATING BEHAVIOR

As in nearly all phyla, recognition and attraction of a sexual partner to promote successful mating depends in malacostracans on a broadcast of identifying behaviors. The display patterns are mainly acoustic, visual, olfactory, tactile and chemical signals. Most of them have been reviewed separately or in their whole in some significant papers (cf. [235, 350–353]).

It must be pointed out that the diverse communication systems seem adapted to the various inhabited spatial localization. Thus, after the first experimental demonstration in the female crab *Portunus sanguinolentus* [379], crustacean sex pheromones inducing precopulatory behavior in the male have been detected in several aquatic species. (cf. for review [353]). Their stimulating effects predominate in small forms such as amphipods (cf. [354–356]), as well as in natantian and reptantian decapods which include large forms (shrimps, lobsters, crabs, etc.) (e.g., [357–360]). A synergistic effect between the pheromone released by the female, olfactory and visual stimuli of either or both sexes is also sometimes required for registering a positive response [361]. At last, among terrestrial and semi-terrestrial species, chemical cues emitted by females appear to be less important than visual, tactile and(or) acoustic signals from males [362, 363].

We have limited the scope of this section to recall the conditions that enable females to become attractive and receptive to males. The releasing and the possible producing site(s) of sex pheromones, as well as their nature and their target organs in the male are also briefly examined.

In addition to local climatic conditions that restrict the copulatory period, the female's attractiveness determining behavioral responses of the males is generally linked to its physiological state, i.e., its molting and ovarian development stages. In some Brachyura (Cancridae and Portunidae), some Astacidea and peracarids, a female is able to mate only when it is soft, shortly after ecdysis [355, 364, 365], while in other Brachyura (Majidae, Xanthidae and Gecarcinidae) mating involves intermolt (hard-shelled) females [364, 366–368]. Detailed informations concerning the ovarian developmental stage of females at the time of mating are lacking. In *Gammarus duebenii,* Hartnoll and Smith [356] mention that "ovarian ripeness" is one prerequisite of the female's attractiveness and that "ovarian condition and molt stage have a synergistic effect". Similar data were reported by Ducruet [355] in two other gammarids. However, unpublished works by Vilotte and Fontaine (cited in [353]) indicate that in *Scyllarus arctus* copulation occurs during previtellogenesis, while in *Carcinus maenas,* a female can remain attractive after exuviation (until A_2), when ovaries are engaged in vitellogenesis. Takayanagi *et al.* [371] identified an ovary-stimulating pheromone that would be released by male organs such as the testis or the vas deferens in the freshwater shrimp, *Paratya compressa.* In some crabs, we have already mentioned that sperm is stored for prolonged periods and can fertilize subsequent spawnings (cf. Section VII, A and for review [235] p. 224).

When a female attracts a male prior to its molt, as in *C. maenas,* presumably because this attraction is initiated pheromonally, the male usually guards her in a precopulatory embrace until she molts and copulation is possible [369]. In *Homarus americanus,* as in the crayfish *Austropotamobius pallipes,* the passive, or cooperative, reaction of the female when encountered by a male is considered as a premating behavior [357, 365]. Likewise, in *Cardisoma armatum,* a semi-terrestrial crab, it is thought that courtship reduces aggressive tendencies in the female [368], but the cues used in sex recognition have not been investigated.

According to Hartnoll and Smith [372], there is no evidence for the production of a male stimulating pheromone in the urine of courted premolt female crab, *Cancer pagurus.* However, behavioral studies indicate that sex pheromone emission is

often associated with urine release from the female antennal gland (cf. reviews [350, 353, 359, 360]). The site of pheromone production is still not well known: Kamiguchi [373] described a sternal gland in female, *Palaemon paucidens,* and Bauchau [353] discovered in *C. maenas* an ectodermic gland more developed in females than in males. It opens in the ureter in the vicinity of the nephropore and seems well-suited to a pheromone release into urine. Information on the chemical nature of crustacean sex pheromones is scarce. Bauchau [353] reported that their molecular weight is ranging from 1000 to 10,000 daltons, according to the species. There are inconclusive data concerning ecdysone (or its derivative), serotonin or peptide as sex attractants ([374, 380], for review [353]). Chemoreceptor sensilla (aesthetascs) on the outer flagellum of antennules are involved in the detection of sex pheromones in several decapods ([353, 358, 375], for review [350]. It has been recently suggested that a hormonal modulation of pheromone-triggered courtship display behavior would exist in the blue crab, *Callinectes sapidus* [376].

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